Sara Ribeiro Mortara

Abundância de samambaias
em metacomunidades

Relacionando padrões e processos com modelos
estatísticos

São Paulo
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Fern abundance in metacommunities
linking patterns and processes with statistical models

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Orientador: Prof. Dr. Paulo Inácio de Knegt López de Prado

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Resumo

Entender como comunidades são estruturadas a partir de um pool de espécies é uma questão central em Ecologia de Comunidades. Diversas abordagens foram propostas para estabelecer a ligação entre os padrões de estrutura de comunidades e os processos que os geram. As regras de assembléia e a abordagem filogenética em ecologia de comunidades são alguns exemplos. Entretanto, o que estas abordagens não levam em conta é o efeito de processos neutros na estruturação de comunidades. Há um consenso de que tanto nicho como neutralidade afetam a estrutura de comunidades e que se deve avaliar a importância relativa de cada um destes processos. A ideia desta tese foi usar modelos estatísticos para representar como processos neutros e de nicho geram padrões em comunidades. No Capítulo 2 propus uma abordagem baseada em modelos hierárquicos através da qual é possível expressar processos neutros e de nicho. A partir disso, foi possível representar hipóteses em que apenas processos neutros afetam a estrutura da comunidade, apenas processos de nicho ou diferentes combinações entre ambos. Usando seleção de modelos, identifiquei qual a combinação de processos melhor explica as abundâncias observadas das espécies. Com isso, mostrei que as comunidades de samambaias em gradientes altitudinais na Serra do Mar no Paraná, Brasil são estruturadas por uma mistura de filtro ambiental, deriva ecológica e limitação de dispersão. O filtro ambiental define as abundâncias das espécies selecionando as melhores estratégias ecológicas das espécies dependendo da altitude. A variação de abundância entre as espécies que compartilham as mesmas estratégias ecológicas é explicada em parte por deriva ecológica e limitação de dispersão e, em parte, por filtro de habitat independente dos atributos das espécies incorporados no modelo. Com isso, delimitei como processos baseados em nicho e neutralidade afetam a abundância das espécies de samambaias ao longo de gradientes altitudinais. No Capítulo 3 usei um estudo de caso para explorar a ideia central da abordagem filogenética em ecologia de comunidades de que é possível inferir os processos que afetam as comunidades com base em padrões locais de estrutura filogenética. Usei a abordagem de modelos proposta no Capítulo 2 para simular comunidades geradas por processos puramente neutros, puramente de nicho e uma combinação hierárquica entre os dois. Encontrei que comunidades geradas apenas por processos de nicho geram estruturas filogenéticas aleatórias na maioria dos casos. A detecção de estruturas filogenéticas aleatórias foi ainda mais frequente nas comunidades geradas por processos puramente neutros e pela combinação de processos neutros e de nicho, não sendo possível a distinção entre estes dois cenários. Desse modo, o estudo de caso mostrou que estruturas filogenéticas não aleatórias são muito pouco plausíveis e que os processos neutros geram uma forte assinatura nos padrões de estrutura filogenética. Com a abordagem proposta nesta tese foi possível delimitar a influência de processos de nicho e neutralidade em comunidades e entender suas consequências em termos dos padrões por eles gerados. A tradução dos diferentes processos em modelos mistos mostrou-se uma ferramenta poderosa para quantificar padrões e construir explicações de como os processos operam juntos.

Abstract

Understanding how communities are assembled from a species pool is a central question in community ecology. Different approaches to link pattern and processes in community ecology were proposed. Some examples are assembly rules and the community phylogenetic approach. However, one aspect not accounted in those approaches is how neutral processes affect community patterns. There is a consensus that both niche and neutral processes affect community assembly and that the goal should be assess the relative importance of each process. The general idea if this thesis was to use statistical models to represent how niche and neutral generate community patterns. In Chapter 2, I proposed a framework based on hierarchical models to express niche and neutral processes. I used this approach to represent hypothesis in which only niche processes affect community structure, only neutral processes or a hierarchical combination of both explains species abundance. By using model selection, I identifyied which combination of processes better predicts observed abundances on local communities. I showed that fern communities across altitudinal gradients at Serra do Mar in Paraná, Brazil are structured by a mixture of environmental filtering, ecological drift and limited dispersal. Environmental filtering defines species abundance, selecting the best ecological strategies of species depending on altitude. Variation on species abundance sharing the same ecological strategies is explained in part by drift and limited dispersal, and in part by habitat filtering independent of species traits considered in the models. Hence, I refined how niche and neutral processes affect fern abundance on altitudinal gradients. In Chapter 3, I used a case study to explore the idea from community phylogenetics of inferring processes affecting communities based on patterns of phylogenetic structure. I used the modeling framework from Chapter 2 to simulate communities built by niche, neutral and combination of both processes. I found that communities based on niche processes are likely to generate a random phylogenetic structure. The detection of random phylogenetic strucure was even more common on communities built solely by neutral processes and combination of both niche and neutral processes. Therefore, the case study showed that a non random phylogenetic strucure is unlikely and that neutral processes strongly affect the outcome of phylogenetic patterns. Based on the framework proposed on this thesis it is possible to delimit the influence of niche and neutral processes on community assembly and to understand what are the consequences in terms of community patterns. Translating different processes into mixed models can be a powerful tool to quantify patterns and built explanations on how the processes operate together.

Sumário

1 — Introdução geral

1.1   Sobre o que é esta tese

Uma das grandes questões em Ecologia de Comunidades é entender quais mecanismos geram diversidade em comunidades biológicas. Existe um padrão de diversidade muito comum: em comunidades biológicas existem poucas espécies que são abundantes e muitas espécies que são raras. Este padrão pode ser descrito por uma curva de rank-abundância e é considerado uma das leis gerais em ecologia (MCGILL et al. 2007). Entender como todas estas espécies co-existem no mesmo local e variam em abundância é uma questão central em ecologia. Existem duas grandes explicações para a diversidade em comunidades biológicas. Uma delas é que as comunidades seriam estruturadas por processos de nicho (HUTCHINSON 1959; DIAMOND 1975), como competição ou filtro ambiental de maneira que prever quais espécies e a abundância com que elas ocorrem seria possível com base nas características das espécies e do ambiente. Outra explicação seria que as comunidades são estruturadas por processos neutros (HUBBELL 2001), como deriva e limitação de dispersão ao acaso, de maneira que seria possível prever a riqueza e abundância de espécies em comunidades simplesmente com base na variação estocástica de nascimentos, mortes e imigração. Esta dicotomia neutro e nicho, que aparece em muitas áreas da ciência como a dicotomia processos estocásticos vs. determinísticos não é recente em ecologia. Desde o início do século XX já existia o debate se comunidades seriam o conjunto de espécies interagindo localmente de maneira fortemente integrada (CLEMENTS 1916) ou se seriam agregações aleatórias de espécies que toleram as mesmas condições ambientais (GLEASON 1926)[1]. Durante as décadas de 1950 a 1980 consolidou-se e prevaleceu uma teoria baseada no nicho e na competição como forças estruturadoras das comunidades (HUTCHINSON 1959; DIAMOND 1975). A partir da década de 1980 esse corpo teórico foi criticado, reavivando mais uma vez o debate sobre o papel de processos determinísticos e aleatórios na montagem de comunidades. Assim, após DIAMOND (1975) propor a ideia clássica de regras de assembleia em

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[1]a ideia de GLEASON (1926) envolve um filtro selecionando espécies que toleram o mesmo ambiente, e a dinâmica neutra seria na escala local onde as assiociaçãoes de espécies coexistindo são definidas pelo acaso.

que o processo central estruturando comunidades seria competição, CONNOR & SIMBERLOFF (1979) propuseram que as comunidades seriam resultado de um processo aleatório, trazendo novamente o debate se comunidades poderiam ser resultado de processos estocásticos à tona. Da mesma forma, a teoria neutra da biodiversidade de HUBBELL (2001) trouxe novamente a dicotomia neutro e nicho para a ecologia de comunidades. Exploraremos o debate neutro-nicho na seção 1.3. Atualmente, pode-se dizer que existe um consenso de que tanto processos de nicho como neutros afetam a montagem de comunidades locais (TILMAN 2004; GRAVEL et al. 2006; ADLER, HILLERISLAMBERS & LEVINE 2007; VELLEND et al. 2014). Ao invés de debater se é um ou outro processo que afetam riqueza e abundância em comunidades, a grande questão em ecologia de comunidades passou a ser a importância relativa de processos de nicho e neutros na estruturação de comunidades. Comunidades são formadas a partir de um pool regional, sendo dispersão e filtros bióticos e abióticos os processos estruturadores. Assim, as comunidades são o resultado do efeito cumulativo destes diferentes processos. Se processos de nicho predominam, veríamos uma maior influência de filtros bióticos e abióticos. Se processos neutros predominam, veríamos uma maior influência de dispersão. Assim, o objetivo desta tese foi entender de que maneira processos de nicho e neutros afetam abundância de espécies de samambaias em gradientes altitudinais. A ideia central é acessar importância relativa do gradiente altitudinal como um filtro ambiental selecionando espécies coexistindo na mesma comunidade local – o componente de nicho – e de deriva e limitação de dispersão – o componente neutro – na definição da abundância das espécies em comunidades locais. As samambaias não dependem de outros organismos para sua dispersão, pois são dispersas pelo vento, constituindo um grupo interessante pra investigar o papel da dispersão e filtros ambientais na assembleia de comunidades. A ideia então é prever padrões de abundância de espécies em comunidades locais com base nos diferentes mecanismos que os geram. Para isto, precisamos de um panorama geral sobre as principais abordagens em ecologia de comunidades que se propuseram fazerem a conexão entre padrão e processo (Seção 1.2) e de uma breve discussão nicho e neutralidade (Seção 1.3). Finalmente, encerramos este capítulo com os objetivos gerais da tese (Seção 1.4).

1.2   Explicando processos olhando para padrões

Uma das grandes questões em ecologia de comunidades é compreender os processos que levam a formação de comunidades a partir de um pool regional (Figura 1.1). Diferentes áreas em ecologia de comunidades se propuseram a fazer uma conexão direta entre padrões e processos evocando alguns conjuntos de regras baseadas em teoria, combinadas a métodos para descrever padrões. Para esta tese, vamos apontar os principais pontos da abordagem de regras de assembleia e da abordagem filogenética em ecologia de comunidades, a qual considero um desdobramento contemporâneo das regras de assembleia.

1.2.1   Regras de assembleia

A questão de como comunidades são formadas a partir de um pool de espécies regional foi colocada como a questão central na abordagem de regras de assembleia. A ideia de que é possível
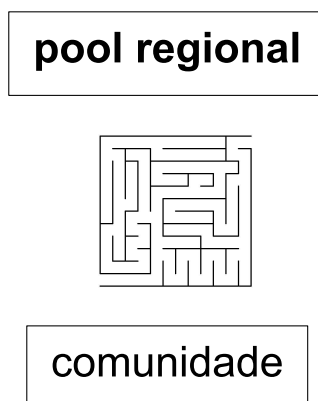
Figura 1.1: Uma das questões em ecologia é encontrar um dos possíveis caminhos para explicar os processos que levam espécies do pool para uma dada comunidade. Extraído de WEIHER & KEDDY (1999).

definir um conjunto de regras a partir das quais as comunidades são formadas foi proposta inicialmente por DIAMOND (1975). DIAMOND (1975) definiu que a composição de espécies em uma dada comunidade seria resultado de interações entre espécies, havendo combinações mais ou menos plausíveis dependendo das interações locais. A ideia de regras de assembleia foi fortemente influenciada pela teoria de biogeografia de ilhas (MACARTHUR & WILSON 1967) e pelo papel central da competição como processo estruturador de comunidades na época devido aos trabalhos de HUTCHINSON (1959) e MACARTHUR (1964); MACARTHUR (1965) que trouxeram a ideia de nicho para o contexto de comunidades. Os trabalhos de Hutchinson e MacArthur não apenas trouxeram a ideia de nicho para comunidades, mas a colocaram como a principal explicação para a estrutura das comunidades. Ainda, a definição de limitação de similaridade (MACARTHUR & LEVINS 1967), segundo a qual espécies competindo por recursos devem apresentar uma diferença fenotípica foi incorporada à abordagem de regras de assembleia. Assim, existiriam combinações de atributos – ao invés de combinações de espécies – mais ou menos plausíveis em comunidades locais (WEIHER & KEDDY 1995). Com a incorporação da informação sobre os atributos das espécies, desenvolveu-se a ideia de que filtro ambiental e competição resultariam em combinações diferentes de atributos em uma comunidade local (WEIHER & KEDDY 1995). Posteriormente, a ideia de analisar o padrão de diferenciação de atributos entre as espécies de uma comunidade para inferir sobre os processos locais – proveniente das regras de assembleia – foi central para o desenvolvimento da abordagem filogenética em ecologia de comunidades, como veremos adiante.

Um ponto importante das ideias sobre regras de assembleia é que elas reforçaram a discussão do papel de interações locais, especialmente competição, na montagem de comunidades. Ao mesmo tempo, estimularam o questionamento do papel central da competição. CONNOR &

SIMBERLOFF (1979), por exemplo, foram pioneiros no questionamento do papel da competição e mostraram que o padrão de diversidade em comunidades poderia ser gerado simplesmente pelo acaso. Este trabalho foi crucial para introduzir o uso de modelos nulos para o teste de padrões em ecologia de comunidades. Após ele, a discussão de que comunidades poderiam apresentar um padrão aleatório veio à tona, seguida de um grande desenvolvimento metodológico em torno de modelos nulos (GOTELLI & GRAVES 1996). No final da década de 90, WEIHER & KEDDY (1999) sistematizaram a ideia da inferência de processos a partir de padrões dentro do arcabouço de regras de assembleia (Figura 1.2). WEIHER & KEDDY (1999) propuseram um modelo verbal de dispersão de atributos a partir do qual seria possível inferir se interações locais ou processos aleatórios afetam comunidades. De acordo com o modelo, o padrão de distribuição dos atributos entre espécies de uma comunidades poderia ser agregado, aleatório ou sobredisperso e cada um seria gerado por diferentes processos. Se o ambiente exerce um filtro forte, as espécies seriam mais parecidas em termos de atributos do que esperado pelo acaso pois o ambiente selecionaria espécies com atributos semelhantes para tolerar as confições ambientais. Já se competição é a força predominante seria esperado que espécies coexistindo fossem mais diferentes em termos de atributos do que esperado pelo acaso pois seria necessária a segregação de nicho para a coexistência de espécies competidoras. Um padrão aleatório seria encontrado quando o filtro ambiental, ou competição não são severos ou em escalas regionais onde o efeito de processos históricos é mais determinante (WEIHER & KEDDY 1995).
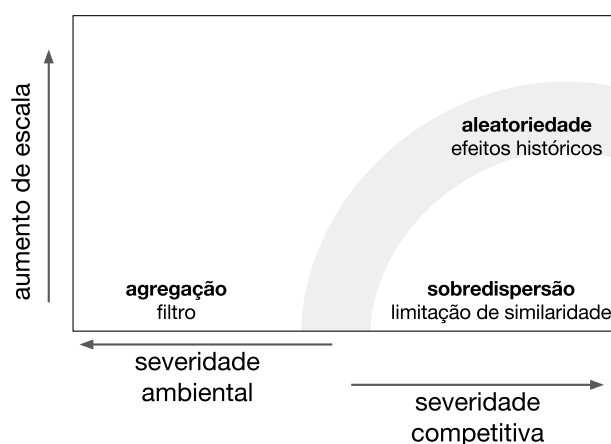
Figura 1.2: Modelo verbal de inferência de processo a partir do padrão dos atributos em comunidades de acordo com regras de assembleia. Traduzido de WEIHER & KEDDY (1999). Se o filtros ambientais exercem uma pressão forte sobre as espécies, seria esperado um padrão agregado dos atributos. Se a competição é forte, seria esperado um padrão sobredisperso dos atributos. Quando a pressão dos filtros ambientais e competitiva são fracas o padrão resultante de atributos seria aleatório. Com o aumento de escala, é esperado que contingências históricas afetem as comunidades, resultando em um padrão aleatório de atributos.

No contexto desta tese é importante ressaltar duas contribuições importantes das ideias de regras de assembleia: apresentar um modelo verbal de conexão entre padrão e processos e

impulsionar os testes de padrões de comunidade confrontando a hipótese do padrão ter sido gerado por acaso. Dessa forma, emergiu-se um consenso de antes de atribuir um padrão a um processo qualquer é preciso testar a probabilidade do erro tipo I. Explorarei a seguir como o modelo conceitual foi incorporado na abordagem filogenética em ecologia de comunidades, mesmo que o reconhecimento de sua origem seja negligenciado na literatura [2].

1.2.2 Regras de assembleia incluindo filogenia

Webb e colaboradores (WEBB et al. 2002) propuseram a ideia de incorporar informação sobre o parentesco entre as espécies para compreender os processos que geram comunidades. O modelo conceitual é muito semelhante ao proposto por WEIHER & KEDDY (1999), porém o padrão observado é o quão espécies são mais ou menos aparentadas do que esperado pelo acaso e como os atributos envolvidos em interações locais evoluíram na filogenia. A ideia de uma abordagem filogenética em ecologia de comunidades foi fortemente influenciada pelas ideias de BROOKS (1985) sobre o uso de filogenias para incorporar o efeito de processos históricos na diversidade em comunidades e de RICKLEFS (1987); RICKLEFS (2004) sobre como a estrutura de comunidades locais é afetada por processos históricos regionais. O argumento pela incorporação de informação histórica e filogenética é que comunidades locais também são afetadas por processos como especiação e extinção (RICKLEFS 1987; RICKLEFS 2004), além do nicho das espécies ser afetado por processos históricos (WIENS & DONOGHUE 2004). De fato, a ideia de que processos históricos afetam comunidades locais já se tornou consolidada em ecologia de comunidades e VELLEND (2010) em sua síntese coloca especiação e extinção como dois dos quatro processos chave afetando comunidades. É importante notar que existem diferentes correntes de incorporação de informação filogenética em ecologia de comunidades e o foco desta tese é a ideia de inferir efeitos da competição ou filtros a partir de padrões de agregação ou sobredispersão filogenética. (WEBB et al. 2002; KRAFT et al. 2007; CAVENDER-BARES et al. 2009).

A ideia central de WEBB et al. (2002) é baseada na hipótese de Darwin que espécies aparentadas entre si não podem co-existir localmente devido à competição. Desse modo, espécies aparentadas devem manifestar atributos e nichos semelhantes e a coexistência entre espécies competidoras depende da existência de segregação de nicho. Se isso é verdade, olhando para o padrão de estrutura filogenética em comunidades locais seria possível separar entre os efeitos de competição e filtro ambiental. De acordo com esta proposta, e na tradição de modelos nulos em ecologia, a estrutura filogenética da uma comunidade reflete o padrão de parentesco entre espécies em comunidades locais podendo ser sobredispersa, agregada ou aleatória. Competição e filtro ambiental resultariam em padrões de estrutura filogenética não aleatórios, enquanto processos neutros resultariam em padrões aleatórios. Devido à limitação de similaridade, em comunidades estruturadas por competição a estrutura filogenética deveria ser sobredispersa já que a coexistência só é possível entre espécies com nichos e atributos diferentes, o que seria

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[2]Veremos que apenas CAVENDER-BARES et al. (2009) e SWENSON et al. (2007) referem-se explicitamente ao modelo conceitual de regras de assembleia, mesmo que o arcabouço teórico de regras de assembleia tenha sido essencial para o desenvolvimento da abordagem filogenetica em ecologia de comunidades.

possível em espécies não aparentadas. Já se filtro ambiental é a principal força estruturando a comunidade, o ambiente selecionaria espécies com atributos semelhantes capazes de tolerar as mesmas confições bióticas. Assim, quando o efeito de filtro abiental é predomindante, a estrutura filogenética deveria ser agregada se a evolução dos atributos é conservada, ou sobredispersa se evolução dos atributos é convergente. Um padrão aleatório seria atribuído à prevalência de processos neutros moldando a comunidade.

Esta abordagem filogenética para interpretar a estrutura de comunidades foi amplamente disseminada e testada, especialmente porque ao mesmo tempo que o arcabouço teórico (WEBB et al. 2002; KRAFT et al. 2007; CAVENDER-BARES et al. 2009) foi proposto, as ferramentas analíticas (WEBB, ACKERLY & KEMBEL 2008; KEMBEL et al. 2010) tornaram-se acessíveis. De maneira análoga, viu-se uma explosão de testes de regras de assembleia após o desenvolvimento dos modelos nulos em ecologia de comunidades (GOTELLI & GRAVES 1996). Os trabalhos testando a validade da abordagem de ecologia filogenética mostram que a conexão entre padrão e processo não é tão clara. Competição, por exemplo, pode gerar uma estrutura filogenética agregada (MAYFIELD & LEVINE 2010; GODOY, KRAFT & LEVINE 2014) ou forças opostas de competição e filtro atuando em conjunto podem levar a uma estrutura filogenética aleatória (VAMOSI et al. 2009; CAVENDER-BARES et al. 2009). Mostrou-se também que a aplicação da abordagem filogenética de conexão entre padrão e processo pode variar dependendo de aspectos como o pool regional de espécies (KEMBEL 2009) e escala (SWENSON et al. 2006; SWENSON et al. 2007). Diante do cenário que os padrões de estrutura filogenética são dependentes da escala temporal e espacial, CAVENDER-BARES et al. (2009) propuseram um modelo conceitual conciliando como diferentes processos e escalas devem afetar comunidades (Figura 1.3).
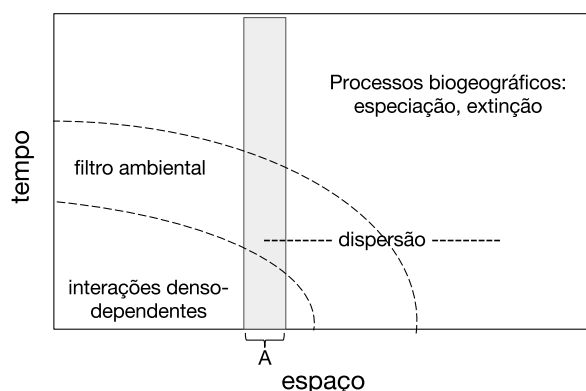
Figura 1.3: Modelo verbal de inferência de como diferentes processos afetam comunidades. Traduzido de CAVENDER-BARES et al. (2009). Baseado em WEIHER & KEDDY (1999) e SWENSON et al. (2007), o modelo estabelece que em escalas espacias e temporais pequenas, interações denso-dependentes prevalecem, filtro ambiental e dispersão são processos importantes na mesoescala e numa escala maior vê-se a influência de processos biogeográficos. Em uma determinada escala – A – diferentes processos afetam a estrutura da comunidade.

CAVENDER-BARES et al. (2009) se basearam nas ideias de WEIHER & KEDDY (1999) e SWENSON et al. (2007) para propor seu modelo verbal. É interessante notar que as questões

de como a intensidade de competição e filtro ambiental pode variar com a escala intrigou pesquisadores trabalhando com regras de assembeia no final da década de 90 e retornou na abordagem filogenética uma década depois (SWENSON et al. 2007). Um mérito importante dos trabalhos da abordagem filogenética foi retomar o modelo conceitual de regras de assembleia. A proposição de CAVENDER-BARES et al. (2009) é que em escalas temporais e espaciais amplas a distribuição das espécies é afetada por processos biogeográficos como especiação, extinção e dispersão. Em escalas menores, o ambiente filtra as espécies que ocorrem nas comunidades, enquanto que em escalas de vizinhança os processos denso-dependentes, como competição, por exemplo, afetam as comunidades. Assim, a distribuição de espécies em uma dada comunidade, como por exemplo na escala A da figura 1.3, depende de diferentes fatores. Separar estes fatores não é uma tarefa simples e deve ser um passo importante para compreender o que gera os padrões de estrutura filogenética em comunidades (CAVENDER-BARES et al. 2009).

No mesmo período em que Webb e colaboradores propuseram as ideias de estrutura filogenética de comunidades, a teoria neutra de HUBBELL (2001) foi proposta. A abordagem de estrutura filogenética foi centrada em separar os efeitos de competição e filtro ambiental e negligenciou como processos neutros podem afetar padrões de estrutura filogenética em comunidades (HARDY 2008; VAMOSI et al. 2009; KEMBEL 2009). Se condiderarmos a dicotomia entre processos neutros e determinísticos na estruturação de comunidades, a abordagem filogenética certamente advogou a favor da prevalência de processos baseados em nicho. Esta dicotomia não é recente, e retomarei os momentos em que esteve em pauta. Chegarei à questão atual de avaliar a importância relativa de cada um dos processos na estruturação de comunidades.

1.3   O debate nicho vs. neutralidade

A questão de que comunidades podem ser estruturadas por um conjunto de regras é recorrente em ecologia de comunidades e em diferentes momentos resultou em uma polarização entre os que defendiam que as regras são determinísticas e os que defendiam que as regras são estocásticas. A disputa clássica entre Clements e Gleason pode ser vista desta maneira. Clements defendia que o ambiente e competição determinam a estrutura de comunidades (CLEMENTS 1916). Em contraste, Gleason defendia que comunidades eram associações aleatórias de espécies com iguais requerimentos (GLEASON 1926). A disputa na época era se comunidades eram formadas por unidades interdependentes ou independentes e pode ser entendida como a disputa determinístico vs. estocástico (NICOLSON, MCINTOSH & NICOLSON 2002). Importante ressaltar que a concepção de comunidade para Gleason é de uma associação aleatória de espécies tolerando as mesmas condições ambientais, o que supõe um filtro ambiental. Entretanto, as dinâmicas populacionais de espécies num dado local são independentes, representando o elemento estocástico, ou melhor, idiossincrático ou não interativo como definido por PUEYO, HE & ZILLIO (2007). Décadas depois, em contraponto às regras de assembleia de DIAMOND (1975) que colocavam a competição como o principal processo estruturando comunidades, CONNOR & SIMBERLOFF (1979) mostraram que comunidades podem apresentar estruturas aleatórias, retomando a discussão do papel de processos estocásticos na formação de comunidades. O trabalho de CONNOR &

SIMBERLOFF (1979) e todo o desenvolvimento de testes de modelos nulos (GOTELLI & GRAVES 1996) contribuíram para a discussão de se comunidades são amostras aleatórias de um pool de espécies ou não. No final da década de 90, uma das críticas da discussão determinismo vs. estocasticidade em regras de assembleia é que se tratava de uma velha discussão – Clements vs. Gleason – com uma roupa nova (FOX 1999). Entretanto, é possível reconhecer que a questão determinismo vs. estocasticidade em regras de assembleia com o desenvolvimento de modelos nulos para testar padrões de estrutura de comunidades foi um passo importante na descrição de padrões em comunidades dentro do contexto teórico de nicho e neutralidade.

Por muitas décadas a visão de que comunidades eram estruturadas por competição prevaleceu. De GAUSE (1934) a CONNELL (1961) com os primeiros experimentos de competição, depois com MACARTHUR (1964) com a definição de limitação de similaridade e as regras de assembleia de DIAMOND (1975), a ecologia passou a ser centrada no papel de interações locais, especialmente competição na assembleia de comunidades. Como apresentamos no início deste capítulo (seção 1.1), em 2001 Hubbell trouxe novamente o debate da influência de processos estocásticos em comunidades. No mesmo período, o paradigma do nicho foi modernizado com a nova teoria de coexistência CHESSON (2000) e a redefinição do conceito de nicho em termos mais rigorosos por CHASE & LEIBOLD (2003). Mais uma vez, se viu crescer o debate se processos determinísticos ou estocásticos afetam comunidades. Talvez um papel importante da formulação da teoria neutra de Hubbell seja a hipótese da equivalência ecológica. Espécies de um mesmo nível trófico seriam equivalentes ecológicas e diferenças de abundância seriam resultado de variações estocásticas de nascimentos, morte e migração. O importante da ideia de equivalência ecológica é que não é necessário evocar competição (ou filtro ambiental) para explicar a estrutura de comunidades, representando um modelo mínimo em ecologia de comunidades (HUBBELL 2005; ROSINDELL, HUBBELL & ETIENNE 2011). Por outro lado, a ideia de que atributos das espécies e filogenia podem ajudar a compreender processos que moldam comunidades proposta por Webb e colaboradores, parte da premissa de que as espécies possuem diferenças que são manifestadas em diferentes atributos e estes atributos podem ser mapeados na filogenia. Nesse contexto, o cerne do debate neutro vs. nicho pode ser considerado o teste da hipótese de equivalência ecológica. Assim, confrontar nicho e neutralidade pode ser feito testando se é preciso evocar os atributos das espécies para explicar a estrutura de comunidades, ou não. Testar a hipótese de equivalência ecológica permitiu ampliar o debate se processos estocásticos ou determinísticos afetam comunidades para a questão de em que nível a equivalência ecológica se aplica (HERAULT 2007; VELLEND et al. 2014).

Explorar em que nível a equivalência ecológica se aplica permitiu reconciliações entre processos estocásticos e determinísticos e delimitar onde neutralidade e nicho afetam comunidades (TILMAN 2004; GRAVEL et al. 2006; ADLER, HILLERISLAMBERS & LEVINE 2007; HERAULT 2007). Ao invés de se perguntar se é um ou outro processo que afeta a estrutura de comunidades, foram propostas por exemplo teorias estocásticas de nicho (TILMAN 2004), hipóteses de que nicho e neutralidade representam um continuum de exclusão competitiva e exclusão estocástica (GRAVEL et al. 2006), combinações hierárquicas de filtro ambiental e estocasticidade demográfica (HERAULT 2007) e combinações entre forças estabilizadoras fortes e fracas (ADLER,

HILLERISLAMBERS & LEVINE 2007). ADLER, HILLERISLAMBERS & LEVINE (2007) argumentam que teorias neutras e de nicho focam em processos complementares que estruturam comunidades e que é possível delimitar casos em que a equivalência ecológica se aplica dentro do paradigma de nicho. Assim, propõem que a coexistência das espécies resultado de um balanço entre o efeito de mecanismos estabilizadores que resultam em diferenças de atributos e devido a forças estabilizadoras fracas que resultam em espécies equivalentes ecológicas. Os diversos trabalhos propondo que processos neutros e de nicho podem operar em conjunto trouxeram uma roupa nova para a discussão polarizada entre nicho e neutralidade após a publicação da teoria neutra da biodiversidade. Desta vez, o passo foi chegar ao consenso de que os dois tipos de processos operam juntos e que objetivo deve ser acessar a importância relativa de cada processo. Estes consensos têm sido promissores.

1.3.1 Distribuição de abundância de espécies no debate nicho vs. neutralidade

O padrão geral de distribuição de abundância de espécies (DAS ou SAD da sigla em inglês para *species abundance distributions*) de poucas espécies abundantes e muitas espécies raras é um exemplo emblemático da disputa nicho vs. neutralidade. Foram propostos diversos modelos para descrever a curva de SAD em comunidades. Alguns dos modelos propostos são puramente estatísticos, outros são modelos mecanísticos (para uma revisão sobre os modelos de SAD ver MCGILL et al. (2007)). Dentre os modelos mecanísticos, podemos ver uma distinção entre modelos que são baseados em partição de nicho (MOTOMURA 1932; SUGIHARA 1980) e modelos que são baseados em dinâmicas neutras (CASWELL 1976; BELL 2000; HUBBELL 2001). O problema dos modelos de SAD para explicar os padrões de comunidade é que tanto modelos baseados em nicho como modelos baseados em dinâmicas neutras se ajustam muito bem aos padrões empíricos (MCGILL et al. 2007). Entretanto, são baseados em premissas completamente diferentes. Modelos de nicho implicam que as espécies mais abundantes são melhores competidoras e por isto ocupam uma porção maior do nicho disponível na comunidade. Se as diferenças entre as espécies podem ser manifestadas em diferenças em relação a determinado atributo, seria esperado uma relação entre o atributo e abundância das espécies (Figura 2.2a). Por outro lado, nos modelos neutros as diferenças de abundância entre as espécies seriam resultado de variação estocástica em taxas demográficas. Assim, seria esperado que as diferenças entre espécies em relação a determinado atributo sejam independentes da variação de abundância, o que implica que as espécies são equivalentes ecológicas (Figura 2.2b). No cenário em que tanto processos neutros como de nicho podem atuar em conjunto afetando abundância das espécies em comunidades, olhar para o quanto o atributo das espécies pode estar relacionado com sua abundância, pode ajudar a separar os efeitos de nicho e neutralidade na estrutura de comunidades.

Uma maneira de testar se os atributos das espécies estão associados com sua abundância pode ser feita por meio de regressões entre atributo e abundância, supondo-se que os atributos usados resumem as adaptações e funções relevantes para as espécies em questão. É possível criar modelos de regressão em que a abundância depende dos atributos das espécies e modelos em que a variação da abundância é independente dos atributos. Ainda, por meio de modelos de regressão hierárquicos é possível representar hipóteses em que a abudância varia estocasticamente e em
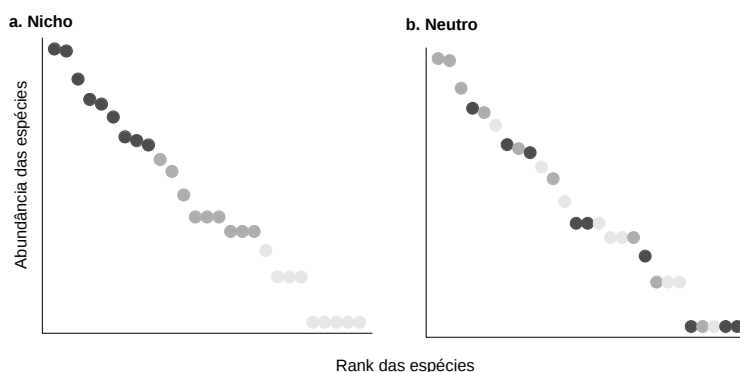
Figura 1.4: Exemplo de como as previsões para a relação dos atributos (em escala de cinza) com abundância das espécies é diferente em modelos de nicho (a) e neutros (b), nos quais se assume equivalência ecológica entre as espécies.

função dos atributos, de modo que é possível representar o efeito conjunto de processos de nicho e neutralidade. Desto modo, é possível criar modelos de regressão representando hipóteses em que apenas processos de nicho afetam a abundância das espécies, apenas processos neutros afetam a abundância ou ambos os processos operam em conjunto afetando a abundância das espécies. Ainda, é possível confrontar múltiplas hipóteses ao mesmo tempo por meio de seleção de modelos e, com isso, testar quais os mecanismos afetam a estrutura da comunidade. Esta tese parte da abordagem de inferência baseada em modelos para explorar duas questões sobre o papel de filtros ambientais, neutralidade e filogenia sobre a distribuição de abundâncias em comunidades.

1.4 Objetivo geral

O objetivo geral deste trabalho foi entender de que maneira processos de nicho e neutros afetam a abundância de espécies. Partimos da ideia de equivalência ecológica entre as espécies para acessar o quanto os atributos das espécies estão correlacionados com sua abundância. Para responder à questão geral deste trabalho usamos dados de comunidades locais de samambaias ao longo de gradientes altitudinais. Os dados foram coletados por PACIENCIA (2008) em três diferentes montanhas na serra do Mar no estado do Paraná, Brasil. É conhecido que a composição de samambaias responde a gradientes ambientais em uma escala local (TUOMISTO, RUOKOLAINEN & YLI-HALLA 2003; KLUGE & KESSLER 2011; ZUQUIM et al. 2014; LEHTONEN et al. 2015) e que dispersão ao acaso é um processo determinante em escala regional (TUOMISTO, RUOKOLAINEN & YLI-HALLA 2003; JONES, TUOMISTO & CLARK 2006). Samambaias são um grupo de plantas dispersas pelo vento por meio de seus esporos. A dispersão pelo vento faz com que as plantas não dependam de nenhum outro organismo biológico para dispersão, sendo um grupo interessante para estudar o papel de dispersão na estruturação de comunidades.

Para responder a questão de o quanto os atributos das espécies afetam sua abundância, desenvolvi modelos estatísticos para separar os efeitos de processos puramente neutros, puramente de nicho e combinações hierárquicas entre os dois na abundância de espécies de samambaias.

No Capítulo 2 usei os modelos estatísticos para testar quais são os processos responsáveis pelos padrões de abundância de samambaias ao longo do gradiente altitudinal. No Capítulo 3 usei os modelos estatísticos ajustados no Capítulo 2 para simular comunidades baseadas em processos de nicho, neutros e combinação entre eles. Então, usei as simulações para testar o quanto os padrões de estrutura filogenética de comunidades refletem os processos pelos quais as comunidades foram geradas, como seria esperado pelo modelo verbal da abordagem filogenética. A ideia geral desta tese, explorada nos próximos capítulos, é que as abundâncias locais das espécies resultam de efeitos aditivos e interações de atributos funcionais das espécies, filtros ambientais e estocasticidade. Proponho expressar estas relações com modelos lineares com efeitos fixos e aleatórios, que depois utilizo para explorar que estruturas filogenéticas podem resultar dessas combinações de efeitos.

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2 — Acessando SADs

Tailoring species abundance distributions with trait-environment correlations

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Abstract

We propose a novel, general test to assess which mechanisms drive SADs. It translates niche and neutral mechanisms into fixed and random effects in a generalized linear mixed model. We applied this methodology to a fern metacommunity along an altitudinal gradient. Hypotheses for niche processes, neutral, and hierarchical combinations of both were tested. We found that although some ecological strategies confer more abundance in a particular altitude on average, drift results in variance in species abundances within the same ecological strategy. We were able to define ecological strategies in fern community based on synthetic and objective traits. Also, our modeling approach unpacks neutrality in drift and limited dispersal mechanisms. Furthermore, predictions from our model fit overly well SADs on each altitude. By adding information of species traits we did not reject the idea of functional equivalence of species, we delimited the influence of neutral processes on community assembly and SADs.

2.1   Introduction

Most species abundance distributions (SADs) in biological communities can be explained equally well by niche and neutral mechanisms (MCGILL et al. 2007). In this case, the problem of distinct processes explaining the same pattern seems to be related to the fact that SADs do not use species identities, which is indeed consistent with the idea of ecological equivalence in neutral theory.

Ecological equivalence implies that trophically similar species are demographically identical (HUBBELL 2001; HUBBELL 2005). Therefore, differences in species abundances should be a result of random birth and death events at local scale that make communities diverge by drift if dispersion is limited (HUBBELL 2001; HUBBELL 2005). In contrast with this view species identities would matter if the lineages evolved a distinctive set of adaptative traits that translate into different niches. In this case species traits should correlate with its abundances, and thus one way to distinguish between neutral and niche processes on SADs would be to assess such correlations. If the ecological equivalence hypothesis is rejected, a strong theory for SADs would be the one that could predict not only the shape of the curve but also if a species would be common or rare based on its traits (MCGILL 2003). For instance, SADs were described as a mixture of abundances of two groups of species, the core (persistent) and satellite (occasional) species (MAGURRAN & HENDERSON 2003). Furthermore, SUPP, KOONS & ERNEST (2015) showed that core and satellite species exhibit different life-history strategies, showing a link between temporal persistence, local abundance, and species life-history traits.

The recognition of different groups of species in the local community is an important step to put SADs in a broader ecological and evolutionary context (MCGILL et al. 2007; SWENSON 2012), but we can go further by asking what defines each group. The obvious choice to identify groups of species in SADs is to look for traits that correlate with their abundances. Thus, placing SADs in a framework that allows to test the ecological equivalence of species would help disentangling niche and neutral mechanisms in predicting species abundances in a community. Assessing trait-environment correlations in community ecology has concerned ecologists for decades since RAUNKIAER (1934) characterization of plant life forms adapted to the environment (see also GRIME 1977; CONNELL 1978). Early development of trait-based approach focused on descriptions of variation of life history traits along environmental gradients. In the past 20 years trait-based approach focused on quantitative measurements of traits for testing non-random trait dispersion in community assembly (SWENSON 2012). The redefinition of the niche concept (CHASE & LEIBOLD 2003), the modern coexistence theory (CHESSON 2000), and Hubbell's proposal of neutral theory (HUBBELL 2001) contributed to the bloom of functional ecology as a test against neutral theories. Empirical and theoretical tests in the context of functional ecology have been followed by a massive analytical development (KRAFT & ACKERLY 2010) from basic functional diversity measures (PETCHEY & GASTON 2002; PETCHEY & GASTON 2007) to different approaches for incorporating functional evenness and divergence (MASON et al. 2005; PAVOINE et al. 2009) and multi-trait analysis (LALIBERTÉ & LEGENDRE 2010), patterns of niche overlap (MASON et al. 2008), mechanisms of environmental filtering (KRAFT et al. 2007; MAYFIELD, BONI & ACKERLY 2009), and trait variation across environmental gradients (SHIPLEY, VILE & GARNIER 2006; CORNWELL & ACKERLY 2009; MESSIER, MCGILL & LECHOWICZ 2010). The remarkable influence of trait-based approaches in plant community ecology could be considered a paradigm shift from species to trait-based ecology (PAVOINE & BONSALL 2011; SWENSON 2012), represented by the emergence of methods and theories as well as the implementation of a global database for plant species traits (TRY) (KATTAGE et al. 2011). Still, much of the trait-based approach focused on species interactions independent of

SADs (SWENSON 2012). Even though there are some efforts of incorporating trait information in SADs (MAGURRAN & HENDERSON 2003; SUPP, KOONS & ERNEST 2015) we can still go further not only asking what defines functional groups in SADs but also what is the relative importance of biological traits versus stochasticity on shaping species abundances.

There is an emerging consensus that both niche and neutral processes are important for community assembly (VELLEND et al. 2014) and that community ecology should advance on how the two processes operate together (GRAVEL et al. 2006; HERAULT 2007). One way of combining neutral and niche processes should be through the delimitation of the set of species in which neutrality applies (SCHEFFER & NES 2006; HERAULT 2007). Emergent Groups are defined as sets of species in a local community which are functionally similar enough with each other that their dynamics is well approximated by neutral theory (HERAULT 2007). Thus, niche differentiation defines each Emergent Group, and within the Emergent Group neutral drift and dispersion limitation define species abundances in the local community. The Emergent Group approach represents the scenario in which neutral and niche processes operate at different levels generating SADs.

Our main goal is to test which mechanisms, in a hierarchy from neutral to niche models, drive fern species abundances in local communities along an environmental gradient, which was sampled in three localities. We start from three potential mechanisms that can explain SADs: (i) purely neutral, (ii) purely niche, (iii) the integration of both with the Emergent Group approach, and derived four hypotheses. The first hypothesis is that neutral processes prevail and species abundances vary among communities randomly, as a result of drift under limited dispersal. Our second hypothesis is that niche processes prevail and species abundances are determined by a set of adaptative traits, which we call an ecological strategy. In this case, species abundances in the local community would be a result of dissimilarities in ecological strategies of species. Also, SADs can change because the optimal strategy can vary along the environmental gradient. Third, species abundances are defined by a combination of niche and neutral processes through Emergent Groups. In the third scenario, ecological strategies of species affect abundance but ecological drift ensues random differences of species abundances within each group. As in the niche scenario, the success of the ecological strategies can depend on the environment. Fourth, assuming that neutrality effects can appear not only as drift within Emergent Groups, we hypothesize that processes generating Emergent Groups could occur combined with limited dispersal. We show how these hypotheses can be translated into fixed and random effects in linear mixed models. We thus propose a novel approach that uses random structure of mixed models to represent drift and limited dispersal in the hypotheses where neutrality operates. We then confronted all hypotheses simultaneously using a model selection framework to test the corresponding models of species abundances.

2.2 Material and methods

2.2.1 Study site and sampling methods

In order to test for trait-environment correlations on species abundances we used abundance data of fern species sampled along an altitudinal gradient in three locations of the Brazilian Atlantic rainforest at Serra do Mar mountain chain, in Paraná State from PACIENCIA (2008). The sampled gradient ranged from sand dune vegetation at the coastal plain (0 to 10 m a.s.l.) to high montane Ombrophilous Forest areas (1,500 m a.s.l.) in three mountain ranges in this ecorregion: Serra da Graciosa (25° 21'S, 48° 54'W), Pico do Marumbi (25° 27'S, 48° 55'W), and Serra da Prata (25° 37'S, 48° 41'W). From 0 to 700 m a.s.l. the climate is subtropical with hot summer and without dry season (Cfa) and with mean temperature during summer above 22° C. Above 700 m a.s.l. the climate is subtropical with warm summer and without dry season (Cfb). Since all mountains are part of the same mountain chain, with controlled distance (from 14 to 41 km distant from each other), we considered sampling sites at the same altitudinal level as replicates from local communities. In fact, floristic similarity among sites at the same altitude is higher than floristic similarity among sites at the same mountain range (PACIENCIA 2008).

Vegetation along the altitudinal gradient varies following changes of soil, humidity, temperature, and precipitation levels. The coastal plain is occupied by scrubland and low forest on poor, white-sand soils. Lowland Ombrophilous Forest occupy the transition between the coastal plain and the mountain range, where the sandy soil has poor drainage but higher fertility. Submontane Ombrophilous Forest occurs from 30 to 400 m a.s.l. and harbors large trees growing on deep clay soils of the hillside. Montane Ombrophilous Forest occurs from 400 to 1,000 m a.s.l. on lithic soils limiting the growth of large trees. Montane forests occur where there are less severe environmental conditions in terms of humidity, temperature, and precipitation. High-montane Ombrophilous Forests occurs from 1,000 to 1,600 m a.s.l. with predominance of lithic soils and where woody stractum is composed by crooked trunks of small size. We used elevation above sea level to represent the altitudinal gradient as a proxy for variation in vegetation type, humidity, temperature, and precipitation. Although altitude represents a set of variables, it is recognized that fern species have specific elevational distributions related to their ecological requirements (MEHLTRETER, WALKER & SHARPE 2010) and fern diversity is correlated with elevation exhibiting a peak at intermediate elevations (KESSLER 2001; CARDELUS, COLWELL & WATKINS 2006; WATKINS JR et al. 2006).

A total of 30 sites were sampled, 10 in each locality, distributed at 0, 10, 50 m, and from 200 to 1,400 at 200 m elevation intervals. In each site, one 20 x 20 m plot was settled. All fern individuals under 2 m from the forest floor were sampled, being included terrestrial ferns, such as terrestrial herbs and tree ferns, hemiepiphyte and epiphyte herbs (only individuals in which the lowermost leaf was up to 2 m from the ground). Abundance was measured as the number of ramets of each species in each sample unit. The study of PACIENCIA (2008) recorded 19,938 individuals belonging to 155 fern species.

2.2.2 Ecological strategy and species abundances

In order to assess trait-environment correlations with species abundances we tested which set of traits define an ecological strategy. We chose three traits that are related to species local abundances and that should respond to environmental changes along the altitudinal gradient. Our choice was based on limitations imposed on ferns due to aspects of their biology such as intolerance to fluctuating conditions and poorly controlled evaporative control (PAGE 2002). Ferns may be less efficient in water use than seed plants due to an inefficient stomatal control, that rely only on passive closure (BRODRIBB & MCADAM 2011). In the absence of strategies to deal with such limitations, ferns have more success on moist habitats where environmental conditions remain constant (PAGE 2002), characteristics such as those found in intermediate altitudes of the studied gradient. In fact, in the context of Emergent Groups, species traits involved in potential challenges faced by plants should be good candidates for delineating Emergent Groups (HERAULT 2007).

We chose two basic leaf traits that can confer advantages on dealing with water limitations: thickness and presence of indumentum (Table 2.1). Thick leaves can store water and increase water use efficiency and the presence of indumentum can reduce water loss from evapotranspiration (WATKINS & CARDELÚS 2012). Thus, thick and/or indumented leaves may enable species to persist on harsh environments such as lowland or high montane forests. Additionally, life form, defined by the subtract a species occupies (e.g., terrestrial, hemiepiphyte, and epiphyte), is an important niche dimension in fern communities segregating species occupying different substrates. Based on the assumption that species within a life form may interact more intensely we included species life form as another trait to define an ecological strategy. We then classified all 155 species based on its traits (see Table S1 in Supporting Information).

Table 2.1: Species traits included in the models to draw an ecological strategy.

Trait	States	Definition
Laminar thickness	Membranaceous and coriaceous.	Laminar thickness was defined in a binary system in which species were separated in membranaceous (from membranaceous to papiraceous) and coriaceous (from cartaceous to coriaceous).
Indumentum	Absence and presence.	Defined as presence or absence of hair and scales on the laminar tissue.
Life form	Terrestrial, epiphyte herb, and hemiepiphyte herb.	Species were classified in terms of habitat preferences for growth. Terrestrial life form includes terrestrial herbs and tree ferns. Epiphyte herbs were separated in epipyte and hemiepiphyte.

2.2.3 Model fitting and selection

To assess the influence of species traits and the environmental gradient on species abundances we translated the niche, neutral and emergent group hypotheses in generalized linear models (GLM)

and generalized mixed-effect models (GLMMs). For all models, we used as response variable the abundances of the 155 fern species recorded in each site and thus absences were accounted as zeros. Confronting a set of statistical models can be done using model selection by identifying which prediction the data support best. We can have models that express alternative hypotheses and then compare them simultaneously (JOHNSON & OMLAND 2004). As a result, based on the selected model we can predict the abundance of a species along the altitudinal gradient and identify which factors best predicts species abundances and, thus, which class of mechanisms prevail in the assemblage of the community. Therefore, we used GLMs and GLMMs as a way to build strong inferences (sensu MCGILL (2003)) on the influence of ecological strategies and altitude on species abundances. By using model selection with GLM and GLMMs we were able to translate alternative hypotheses in competing models. GLMMs have been widely used in Ecology and Evolution since it is common to have non-normal biological data that involves random effects (BOLKER et al. 2009). Here, we used the random structure of mixed models to represent alternative hypotheses involving neutral processes such as drift and limited dispersal.

To test our hypotheses we built 34 models representing each of our general hypotheses (Box 2.1 and Table 2.2). Models corresponding to the idiosyncratic, neutral dynamic, Emergent Groups, and Emergent Groups with limited dispersal hypotheses were built using GLMM approach. Each term in the models represent a particular process. Models corresponding to purely niche effects were built using GLMs. We assumed that neutrality within Emergent Groups, limited dispersal and ecological drift can be expressed as a random factor in the GLMMs since we are incorporating random variation of abundance from the overall mean value in a particular level. Species abundances were modeled as a Poisson variable with a logarithm link function. The effect of altitude was expressed as a fixed effect in niche and Emergent Groups models and included as a second-order polynomial, since the study of PACIENCIA (2008) detected unimodal relationships of abundances with the altitudinal gradient. Niche theory predicts that differences in species abundances should be due to differences in species traits in response to the environment. Therefore, the use of ecological strategies as fixed effects means that species sharing the same ecological strategy would have the same linear response in terms of abundance along the altitudinal gradient. In contrast, in a neutral community abundances of all species drift randomly around the same mean value. If so, abundance of each species would be a realization of the same random process, which would translate into a random effect of species identities in a linear model. We translated the effect of drift under limited dispersal as a random effect of species identities restricted to localities (i.e., regional communities at different mountain ranges) representing low means of movement of individuals within the metacommunity. In addition, for the models combining niche and neutral effects we also added a random term to represent variation of species abundance among sampling sites at the same altitude (i.e. triplets of sites that share the same position at the gradient across localities). This is a random term representing variation of species abundance due to filtering processes that is not accounted by filters specified on fixed effects.

Box 2.1 — Predictions for each general hypothesis.
■ **Idiosyncratic**

Differences in abundance are due random variation among localities and species.

■ **Neutral dynamic**

(i) Differences in species abundances are due to limited dispersal among localities Local SADs are the result of random variation of abundances at each locality.

■ **Niche**

(i) Absolute fitness differences among strategies: the ecological strategy of a species affect species abundances but does not depend on altitude. (ii) Trait-environment correlation: the effect of ecological strategies on abundance are positive in some altitudes but negative in others.

■ **Emergent Groups**

(i) Absolute fitness differences among strategies, but there is random variation in species abundances among species within the same ecological strategy. (ii) Trait-environment correlation but there is stochastic differences in species abundances among species with the same ecological strategy.

■ **Emergent Groups with limited dispersal**

(i) Emergent groups with absolute fitness differences with limited dispersal among localities: abundances are affected by ecological strategies but also have a random variation among species. Species abundance also vary due to filtering process independent of species traits. (ii) Emergent groups model with limited dispersal among localities. Same as latter but without random variation among sites. (iii) Emergent groups model with trait-environment correlation and with limited dispersal among localities. Species abundance also vary due to filtering process independent of species traits. (iv) Emergent groups model with trait-environment correlation and with limited dispersal among localities.

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Model fitting was done using numerical routines to approximate maximum likelihood (BATES et al. 2015). The models were then compared using the Akaike Information Criteria (AIC), a measure of support by the data. The model with lowest AIC value was selected as the most plausible statistical hypothesis and models with ΔAIC differences less than two were considered equally plausible. Data analysis was done on R software (R CORE TEAM 2015), using the package lme4 (BATES et al. 2015).

2.2.4 Generating SADs

In order to identify the effects of ecological strategies on SADs, for each altitudinal level, we built rank-abundance diagrams using the mean relative abundance of each rank among the mountain ranges. We then compared these empirical values to the rank-abundances diagrams of

Table 2.2: Fixed and random effects included in each group of models. L=localities; SP=species; S=sampled sites, altitude as categorical variable or A=altitude as a second order polynomial; ES = ecological strategy, which is a factor with one level for each combination of traits observed in the species (see Table 2.1); |=conditioned to; ∗=interacting with.

General hypothesis	Effects		Number of models
	Fixed	**Random**	
■ Idiosyncratic		L+SP	1
■ Neutral dynamic		1|SP+L|SP	1
■ Niche	ES		8
	ES∗A		
■ Emergent Groups	ES	1|SP	8
	ES∗A	1|SP	
■ Emergent Groups with limited dispersal	ES	1|SP+L|SP+S|SP	16
	ES	1|SP+L|SP	
	ES∗A	1|SP+L|SP+S|SP	
	ES∗A	1|SP+L|SP	

the abundances predicted by the selected model at each site.

2.3 Results

2.3.1 Neutral dynamic, niche, and Emergent Groups

We observed that species traits affect species abundance and interact with altitude, but we still detected the effect of Emergent Groups and limited dispersal. The best model have the effects of ecological strategy interacting with altitude, filtering independent of species traits, and also effects of neutral drift within localities (Table 2.3, see also Tables S2 and S3). It is worth noting that the set of models that express the Emergent Group and limited dispersal hypotheses accumulated almost all the evidence weight (sum of Akaike weight=0.9999, with the weight of 0.9624 for the best model). In the selected model Emergent Groups were defined by combinations of life form and leaf thickness: (i) terrestrial species with membraceous leaves; (ii) terrestrial species with coriaceous leaves; (iii) hemiepiphyte species membraceous leaves; (iv) hemiepiphyte species coriaceous leaves; (v) epiphyte species with membraceous leaves; (vi) epiphyte species with coriaceous leaves.

The interaction between strategy and altitude highlights that species mean abundances within some combination of traits are higher in some altitudinal levels but lower in others (Fig. 2.1). Individuals of terrestrial and hemiepiphyte species with membranaceous leaves present an abundance peak at intermediate altitudes of the gradient (600 to 800 m). Individuals with coriaceous leaves present higher values of abundance on lowland forests, with decreasing abundance values following the decrease in altitude (Fig. 2.1a-d). Whereas terrestrial and hemiepipyte species presented similar patterns of abundance along altitudinal variation, we observed a distinct pattern for epiphyte species. In general, epiphyte species tended to be more

Table 2.3: Model selection showing models with Akaike weight > 0.001. For a complete table of model selection results see Table S2. EG=Emergent Group; L=localities; SP=species; S=sampled sites, altitude as categorical variable or A=altitude as a second order polynomial; ES=ecological strategy; ES 01 = laminar thickness and indumentum; ES 02 = indumentum and life form; ES 03 = laminar thickness and life form; ES 04 = laminar thickness, indumentum and life form; |=conditioned to; ∗=interacting with.

Model	Effects	AIC	ΔAIC	df	Weight
EG with limited dispersal	ES 03 * A + 1|SP + L|SP + S|SP	19150.5	0.0	15	0.9624
EG with limited dispersal	ES 02 * A + 1|SP + L|SP + S|SP	19157.3	6.8	15	0.0316
EG with limited dispersal	ES 03 + 1|SP + L|SP + S|SP	19162.0	11.6	7	0.0030
EG with limited dispersal	ES 02 + 1|SP + L|SP + S|SP	19162.9	12.4	7	0.0019

abundant on extreme altitudes of the gradient (Fig. 2.1e-f). The pattern is more conspicuous for epiphyte species with coriaceous leaves. It is remarkable that above 1,200 m epiphyte species are predominantly abundant. Although some combination of traits confer, on average, high values of abundance depending on the altitude, there was wide variation among abundances of species of the same Emergent Group as shown by wide standard errors. The standard errors of predicted values matched this variation (Fig. 2.1) which was captured by the interaction between random effects of species with sites and with localities. In the model the interaction between species and sites accounted for random variation in abundances caused by drift under limited dispersal. The interaction between species and localities accounted for variation in species abundance caused by a habitat filter independent of species traits.

2.3.2 Generating SADs

When analyzing the general pattern of SADs along the altitudinal gradient we observed high dominance on extreme altitudes – lowland and high montane forests – and more evenness on intermediate altitudes (Fig. 2.2). The selected model provided an excellent fit of observed values of abundance on SADs across the gradient (Fig. 2.2). As shown by the selected model, SADs reveal that certain combination of traits are associated with the changes of species abundances at along the environmental gradient. At sites ranging from 400 to 1,000 m a.s.l. most of abundant species had membranaceous leaves, independently of the life form (Fig. 2.2e-h). In contrast, at lowest and highest altitudes, species with coriaceous leaves were among the most abundant recorded. Terrestrial species with coriaceous leaves were abundant from 0 to 200 m (Fig. 2.2a-d) and from 400 to 1,000 m (Fig. 2.2e-h) terrestrial species with membranaceous leaves were abundant. Additionally, from 10 to 1,000 m we always found a hemiepiphyte species with membranaceous leaves among the three most abundant species in the communities (Fig. 2.2b-h). In contrast, hemiepiphyte species with coriaceous leaves, are, generally, among rare species at sites above 600 m (Fig. 2.2g-j). It is notable the occurrence of epiphyte species among the most
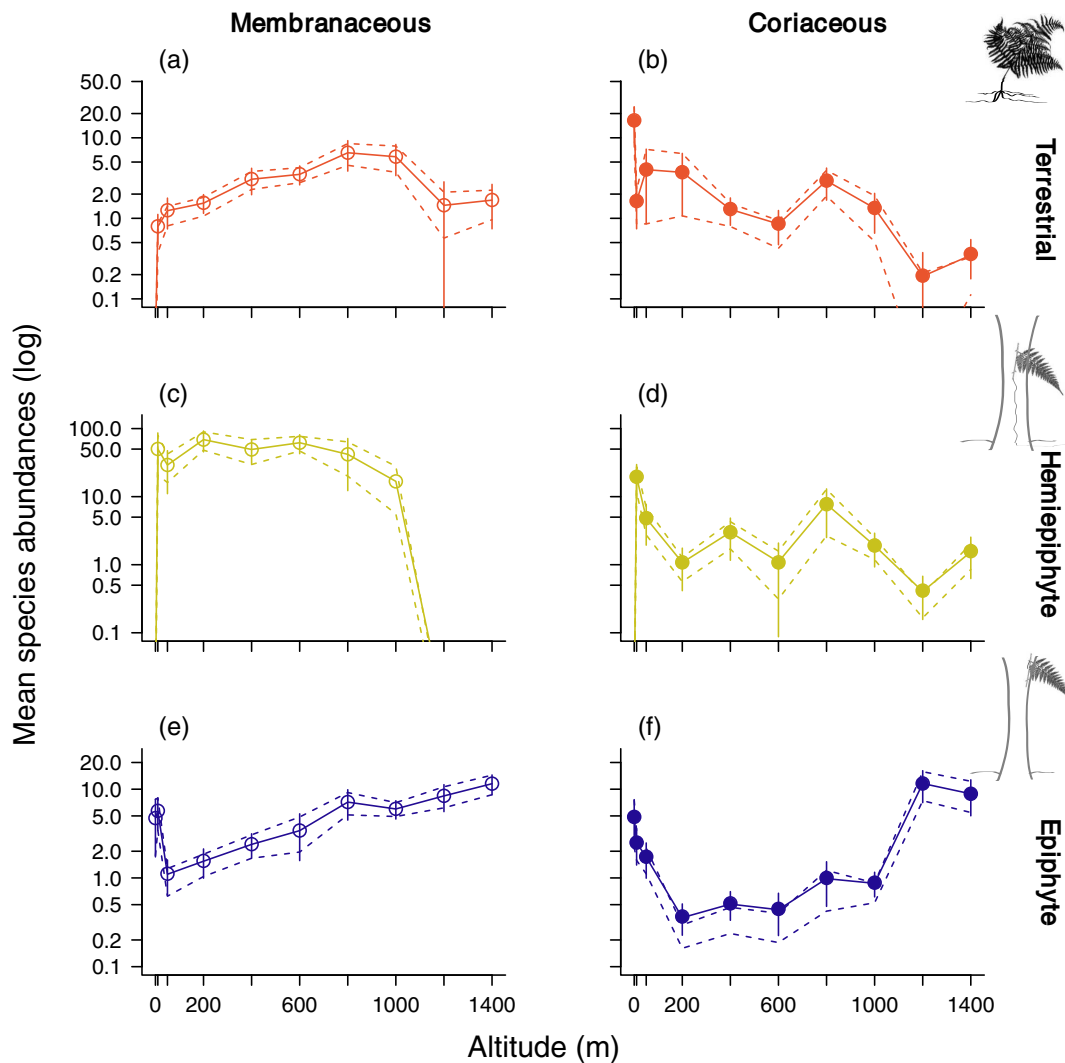
Figure 2.1: Mean abundances of fern species (log) within each trait along the altitudinal gradient in a Brazilian Atlantic Rainforest of Paraná State. Terrestrial individuals (a-b), hemiepiphyte individuals (c-d), epiphyte individuals (e-f). Solid lines represent abundance values predicted from the select model, and dashed lines represent ± predicted standard errors.

abundant species at sites above 1,000 m (Fig. 2.2i-j), as well as the increasing dominance of this life form at high altitudes. In summary, as predicted by the selected model, general patterns of abundance among species that share the same combination of traits are associated, on average, with higher abundances depending on the altitude. Although, abundances vary markedly among species that share the same trait combination, which is consistent with the prediction of the selected model including the random drift within Emergent Groups.

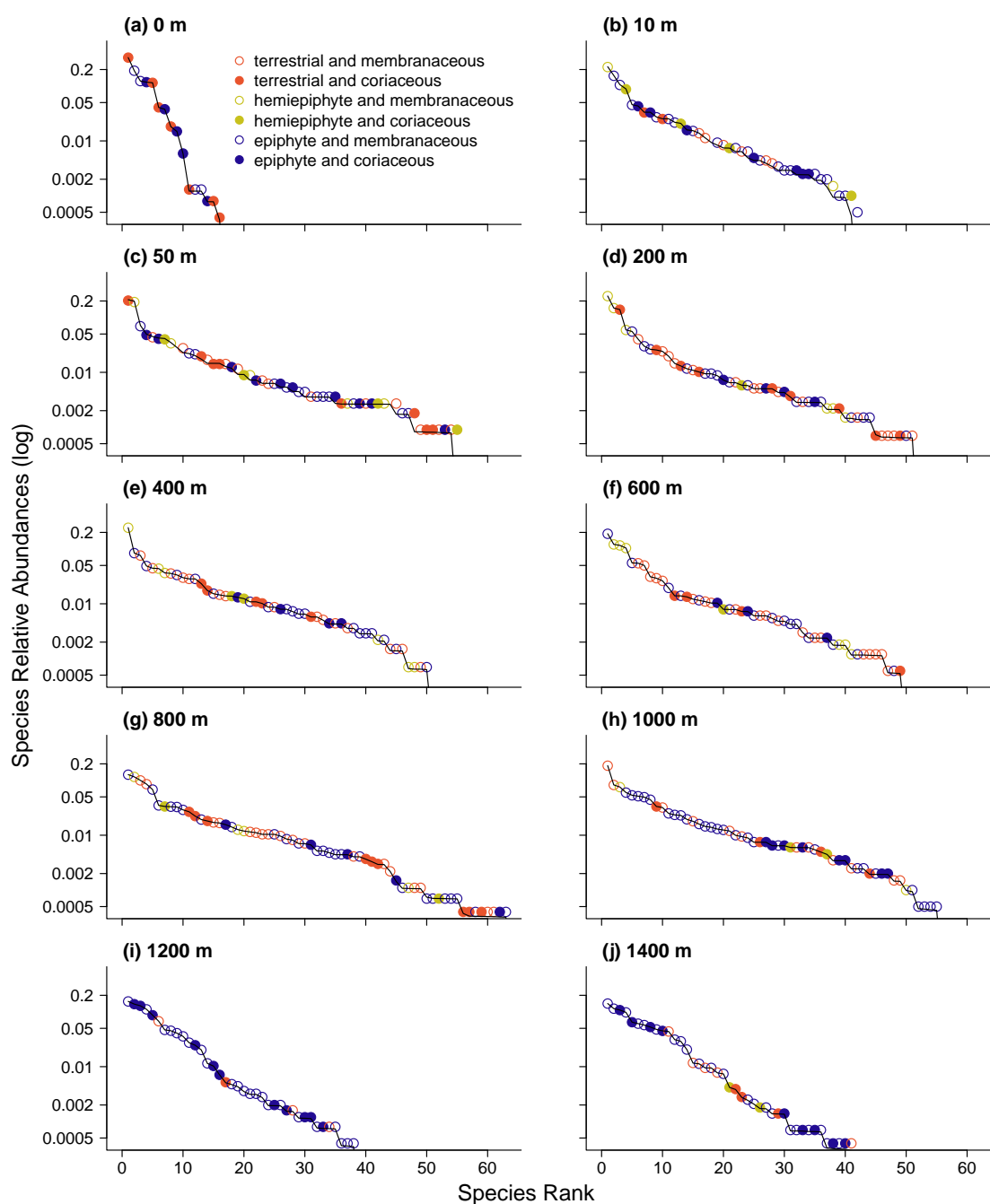Figure 2.2: Fern species relative abundance distributions (log) along the altitudinal gradient in a Brazilian Atlantic Rainforest of Paraná State. Black solid line represents predicted values by the selected linear mixed model, that includes an interaction between ecological strategies and altitude (fixed effects) and random variation among species within the same strategies and within sites and localities

2.4 Discussion

Analyzing only the SADs of fern the communities one would observe the remarkable change in dominance along the altitudinal gradient, that some ecological strategies are associated with high abundance values, and that there there is still great variance in abundance among species that share the same ecological strategy. With our modeling approach we can not only predict the shape of the SADs depending on the altitudinal gradient but also the different niche and neutral mechanisms generating it. By our model we can predict the mean abundance of a species given its ecological strategies and its position on the altitudinal gradient, representing the niche effect. Additionally, there is environmental filtering independent of assessed traits defining variation on species abundance. Still, remains variability that can be attributed to random drift, supporting the idea of Emergent Groups, and through random variation of species abundances on localities. We demonstrated that whereas the ecological equivalence assumption does not apply, there is still influence of neutral processes, such as drift within Emergent Groups and limited dispersal, on community assembly. Therefore, our model express the assembly of fern communities as combination of selection and drift (VELLEND 2010). The gradient acts as an environmental filter exerting a selective force on which species and trait frequencies will succeed in a given local environment (WEBB et al. 2010). Alternatively, within each emergent group, species may have recruitment differences due to stochastic colonization rates or limited dispersal, generating stochastic changes in species abundances (GRAVEL et al. 2006; WEIHER et al. 2011).

2.4.1 Tailoring SADs with mixed models

By using mixed-effect models we could describe SADs of each local community accurately as a combination of SADs of different functional groups with random variation. In our models, the abundances of each species in samples of each community are described as a Poisson process. Species with different ecological strategies have different mean predicted abundances at each point of the environmental gradient. The random effects allow mean abundances to vary among species and sites within each ecological strategy at each environment. The predicted SADs are then the abundances predicted by all these fixed and random effects, that express niche and neutral processes. Therefore our model applies the decomposing of SADs based on species traits (MAGURRAN & HENDERSON 2003) in the context of Emergent Groups (HERAULT 2007).

The classic hollow curve pattern of the SADs is generated by differences in fitness among species and alternative strategies lead to negative skew (MAGURRAN & HENDERSON 2003). Thus, random variation in species ranks on SADs for the same ecological strategy is due to random demographic rates and random placement of species in localities. The consequence for SADs is that random processes generate variation in negative skewness. MAGURRAN & HENDERSON (2003) attributed the negative skew to niche subdivision, without having to invoke neutrality. On the other hand, according to neutral theory (HUBBELL 2001) negative skew would be a result of community size and immigration rate. Our model makes an accurate prediction for SADs based on how niche and neutrality affect community assemblage and SAD empirical skewness.

Approaches based on functional traits have been used to demonstrate the importance of environmental filtering in structuring diverse ecological communities (LAVOREL & GARNIER 2002; BARALOTO et al. 2012). Even with a lot of methodological development in recent years it is not easy to disentangle between trait versus neutral influences and methods fail to detect the signature of processes such as dispersal (KEMBEL 2009). Linear models with random effects associated to species is an effective tool to describe joint responses of species groups to environmental gradients (JACKSON et al. 2012). We extended this idea choosing effects that can be interpreted as outcomes of neutral dynamics and niche processes. Our modeling approach decomposes the effects of neutrality in drift and limited dispersal mechanisms. Drift is depicted by random variation in abundance among species that share the same ecological strategy, while limited dispersal is depicted as random variations of abundance of each species at mountain ranges. There is still variation of species abundance across sampling sites that is attributed to habitat selecion independent of species traits. Our method is analogous to a variance partitioning of environmental and spatial variables (GILBERT & LECHOWICZ 2004) that decouples neutral and niche processes into distance and environment componentes. The advantage of our proposal is that each term in the model represent a particular processes and through model selection one can identify which combination of processes better explain species abundance. Therefore, linear mixed-effect models provides a straightforward way to translate hypotheses on the effects of niche, drift and dispersal on species abundances in competing statistical models. Information indexes like AIC can then be used to express the support provided by data to each model (BURNHAM & ANDERSON 2002; JOHNSON & OMLAND 2004). The simultaneous comparison of competing models that map to alternative hypotheses grounded in the theory is the 'golden standard' of model-based inference (HILBORN & MANGEL 1997) and a much-needed improvement to phenomenological 'curve-fitting' to SADs (MCGILL 2003).

2.4.2 Niche and neutrality at play in fern communities

We defined ecological strategies for fern communities based on synthetic traits that are relevant for community assembly. Laminar thickness and life forms are obvious traits for plant ecologists that we can in fact relate with differences in species abundances besides being. Additionally, they are important traits in an evolutionary context since one of the most important event of fern diversification is attributed to the arise of strategies to cope with new niche space and low-light and water requirements in angiosperm-dominated forests in Cretaceous and Cenozoic periods. (SCHNEIDER et al. 2004; SCHUETTPELZ & PRYER 2009). Given that an ecological strategy predicts different abundances depending on the position of the gradient that a species is, we infer that there are tradeoffs on having some ecological strategies. Having thick leaves, for instance, may be a good characteristic for dealing with more severe conditions in terms of water availability – on lowland forests and above 1,200 m – as predicted by our model, specially in the case of ferns that have reduced water efficiency (PAGE 2002; WATKINS & CARDELÚS 2012; VASCO, MORAN & AMBROSE 2013). However, having thick leaves on moist and moderate environments do not result in more success in terms of local abundances. Indeed conservative water use strategies of ferns seem to constrain their utilization of light on low-light forests

(ZHANG et al. 2009), representing a light use vs. water storage tradeoff. Actually, as predicted by our model it is worth having thin leaves to be successful in intermediate positions of the altitudinal gradient.

Our results also highlighted the importance of life form for the average fitness of fern species. Different predicted abundance values within the same ecological strategy among life forms reinforces the assumption that terrestrial and epiphyte ferns can have different physiological and life cycle characteristics to deal with water and nutrient availability (PAGE 2002; WATKINS & CARDELÚS 2012). In general, epiphyte species deal better with limited water and nutrient sources than terrestrial species (PAGE 2002; SCHUETTPELZ & PRYER 2009; WATKINS & CARDELÚS 2012). This can explain why, in general, epiphyte species despite of the leaf trait are more abundant on the extremes of the gradient, specially on high altitudes. In addition to leaf traits epiphyte fern species can also count with the gametophyte traits to cope with low water availability since it seems that epiphyte fern gametophytes are more resistant to survive on harsh environments than terrestrial gametophytes (WATKINS & CARDELÚS 2012). Thus, survival of gametophyte combined with sporophyte strategies can make epiphyte species reach high values of abundance at the extremes of the gradient. Alternatively, terrestrial ferns have unique chemical compounds conferring advantage on forest floor where there is low-light available (KAWAI et al. 2003) and where species with thin leaves can succeed. Photoreceptors in terrestrial ferns enhance light sensitivity by orienting leaves and chloroplasts and have contributed to proliferation of ferns on low-light conditions (KAWAI et al. 2003). Having these compounds may offset strategies of having thick leaves, contributing to high abundances of terrestrial ferns on intermediate portions of the gradient, under dense canopy cover. Again, there may be a light use vs. water storage tradeoff for explaining why terrestrial ferns with thicker leaves present higher abundance values only on the low extreme of the gradient. The biology of hemiepiphyte is still poorly known in comparison with other life-forms (WATKINS & CARDELÚS 2012). Nevertheless we identified an abundance pattern different from epiphtyes with some similarities with terrestrial species, supporting that hemiepiphyte species form a distinct functional group. There are few hemiepiphyte species with coriaceous leaves, and those with membranaceous leaves are very abundant compared to other life forms on intermediate altitudes. Wherever hemiepiphyte with thin leaves occur, mostly on the low to medium altitudes, they are very abundant, but at highest positions of the gradient they do not occur. Differently from other studies on fern communities that separates the assemblage into terrestrial and epiphyte components (WATKINS JR et al. 2006; KLUGE & KESSLER 2011), our study identified hemiepiphyte species as a functional group apart. Since most hemiepiphytes spend only part of its life cycle as an epiphyte and can produce spores both on ground and on trunks (JP pers. obs.), they can override terrestrial and epiphytes abundances where they occur.

Finally, in an historical context we can count three main strategies comprise fern success: evolution of epiphytism, features that allow ferns withstand dry conditions and a unique photoreceptor that enhanced fern sensibility to light (SCHNEIDER et al. 2004; SCHUETTPELZ & PRYER 2009). These life history strategies of ferns that allowed them to persist and diversify on forest environments seem to be related to local ecological strategies of species that can

define the Emergent Groups in local communities. The best supported models ascribed variation of abundances within Emergent Groups to joint effect of drift, dispersal limitation, and environmental filtering independent of species traits. Variance in species abundances are due to limited dispersal at a regional scale and habitat selection at a local scale. The fraction of environmental filtering not accounted for traits we incorporated in the model can be related to selection in the gametophyte generation. Since ferns are wind dispersed plants it may be counterintuitive to consider that limited dispersal can play an important role in community assembly. However, it has been known that fern communities can be affected by limited dispersal (TUOMISTO, RUOKOLAINEN & YLI-HALLA 2003; KARST, GILBERT & LECHOWICZ 2005; JONES, TUOMISTO & CLARK 2006) in an ecological scale and it has been recognized that some groups of ferns present conspicuous patterns of restricted speciation and diversification patterns driven by dispersal limitation (KORALL & PRYER 2014; LABIAK et al. 2014; SUNDUE et al. 2014) in an evolutionary scale. Since the limited dispersal is a stochastic component in our model it seems reasonable to consider that limited dispersal is randomly affecting spore dispersal at a regional scale and the local filtering can be related to variation in gametophyte establishment depending on the sampling site. Therefore, species are being limited regionally by a neutral process and locally by niche processes.

2.4.3 Concluding remarks

Rebuilding SADs from abundances predicted by our linear mixed model allowed us to understand how aspects of fern biology can influence community patterns. We identified the importance of tradeoffs on strategies for reducing water loss across the altitudinal gradient. Among species with the same strategy, we show that neutral drift and limited dispersal also affect differences in abundances as well as a local filtering component not controlled by species traits. We proposed a mechanism that explains species abundances in the community combining neutral and niche-based approaches. Hence, we simply refined the scope of neutral processes affecting species abundances with the concepts of Emergent Groups and limited dispersal. In this context, one promising question to be answered is how ecological traits that define Emergent Groups in a fern community evolved and how phylogenetic relatedness of species affects the definition of the Emergent Groups. Placing Emergent Groups in an evolutionary context may help understand integration levels of niche and neutral processes in community assembly.

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Supplementary material

Table S1. List of species collected in PACIENCIA (2008) study with its traits.

Species	Indumentum	Laminar thickness	Life form
Abrodictyum rigidum	absent	membranaceous	terrestrial
Actinostachys pennula	absent	coriaceous	terrestrial
Adiantopsis regularis	absent	cartacea	terrestrial
Adiantum abscissum	present	membranaceous	terrestrial
Alansmia reclinata	absent	membranaceous	epiphyte
Alsophila setosa	present	coriaceous	terrestrial
Alsophila sterrestrialnbergii	present	coriaceous	terrestrial
Anemia phyllitidis	absent	coriaceous	terrestrial
Anetium citrifolium	absent	coriaceous	epiphyte
Arachniodes denticulata	present	cartacea	terrestrial
Asplenium auriculatum	present	coriaceous	epiphyte
Asplenium feei	present	coriaceous	terrestrial
Asplenium harpeodes	absent	membranaceous	epiphyte
Asplenium incurvatum	absent	cartacea	epiphyte
Asplenium kunzeanum	absent	membranaceous	terrestrial
Asplenium lacinulatum	absent	membranaceous	terrestrial
Asplenium martianum	absent	membranaceous	terrestrial
Asplenium mucronatum	absent	membranaceous	epiphyte
Asplenium muellerianum	absent	membranaceous	epiphyte
Asplenium oligophyllum	absent	membranaceous	epiphyte
Asplenium pseudonitidum	absent	membranaceous	terrestrial
Asplenium pterrestrialopus	absent	membranaceous	epiphyte
Asplenium scandicinum	absent	membranaceous	epiphyte
Asplenium serra	absent	membranaceous	epiphyte
Asplenium serratum	absent	coriaceous	epiphyte
Asplenium triquetrum	absent	membranaceous	terrestrial
Asplenium uniseriale	present	membranaceous	terrestrial
Blechnum binervatum subsp. acutum	absent	coriaceous	hemiepiphyte
Blechnum brasiliense	absent	coriaceous	terrestrial
Blechnum cordatum	absent	coriaceous	terrestrial
Blechnum sampaioanum	absent	membranaceous	terrestrial
Blechnum schomburgkii	absent	coriaceous	terrestrial
Blechnum serrulatum	absent	coriaceous	terrestrial
Campyloneurum acrocarpon	absent	coriaceous	hemiepiphyte
Campyloneurum lapathifolium	absent	membranaceous	hemiepiphyte
Campyloneurum nitidum	absent	coriaceous	hemiepiphyte
Campyloneurum rigidum	absent	coriaceous	hemiepiphyte
Ceradenia albidula	present	coriaceous	epiphyte
Cochlidium punctatum	present	coriaceous	epiphyte
Cochlidium serrulatum	present	coriaceous	epiphyte
Ctenitis pedicelata	present	membranaceous	terrestrial

Species	Indumentum	Laminar thickness	Life form
Cyathea atrovirens	present	coriaceous	terrestrial
Cyathea corcovadensis	absent	coriaceous	terrestrial
Cyathea delgadii	present	membranaceous	terrestrial
Cyathea leucofolis	present	coriaceous	terrestrial
Cyathea phalerata	absent	membranaceous	terrestrial
Danaea moritziana	absent	membranaceous	terrestrial
Danaea nodosa	absent	coriaceous	terrestrial
Dennstaedtia dissecta	present	membranaceous	terrestrial
Didymochlaena truncatula	present	membranaceous	terrestrial
Didymoglossum krausii	present	membranaceous	epiphyte
Didymoglossum repiphytetans	present	membranaceous	epiphyte
Diplazium ambiguum	absent	membranaceous	terrestrial
Diplazium cristatum	absent	membranaceous	terrestrial
Diplazium lepiphytetocarpon	absent	membranaceous	terrestrial
Diplazium plantaginifolium	present	membranaceous	terrestrial
Doryopterrestrialis acutiloba	absent	coriaceous	terrestrial
Elaphoglossum brachyneuron	present	coriaceous	epiphyte
Elaphoglossum chrysolepiphyteis	present	membranaceous	epiphyte
Elaphoglossum crassinerve	absent	membranaceous	epiphyte
Elaphoglossum didymoglossoides	present	membranaceous	epiphyte
Elaphoglossum iguapense	absent	membranaceous	epiphyte
Elaphoglossum lingua	absent	coriaceous	epiphyte
Elaphoglossum macrophyllum	absent	coriaceous	epiphyte
Elaphoglossum nigrescens	absent	membranaceous	epiphyte
Elaphoglossum ornatum	present	coriaceous	epiphyte
Elaphoglossum paulistanum	absent	coriaceous	epiphyte
Elaphoglossum sp.	NA	NA	epiphyte
Elaphoglossum squamipes	present	coriaceous	epiphyte
Eupodium laevis	absent	membranaceous	terrestrial
Grammitis fluminensis	present	coriaceous	epiphyte
Hecistopterrestrialis pumila	absent	membranaceous	epiphyte
Hymenophyllum asplenioides	absent	membranaceous	epiphyte
Hymenophyllum caudiculatum	absent	membranaceous	epiphyte
Hymenophyllum elegans	present	membranaceous	epiphyte
Hymenophyllum fragile	present	membranaceous	epiphyte
Hymenophyllum fucoides	present	membranaceous	epiphyte
Hymenophyllum hirsutum	present	membranaceous	epiphyte
Hymenophyllum magellanicum	present	membranaceous	epiphyte
Hymenophyllum microcarpon	present	membranaceous	epiphyte
Hymenophyllum polyanthos	absent	membranaceous	epiphyte
Hymenophyllum pulchellum	present	membranaceous	epiphyte
Hymenophyllum vestitum	present	membranaceous	epiphyte
Lastreopsis amplissima	present	membranaceous	terrestrial
Lellingeria apiculata	present	membranaceous	epiphyte
Lellingeria brevistipes	poucos	membranaceous	epiphyte
Lellingeria depiphyteressa	poucos	membranaceous	epiphyte
Leucotrichum organense	present	coriaceous	epiphyte
Leucotrichum schenkii	present	coriaceous	epiphyte

Species	Indumentum	Laminar thickness	Life form
Lindsaea arcuata	absent	coriaceous	terrestrial
Lindsaea bifida	absent	membranaceous	epiphyte
Lindsaea botrychioides	absent	coriaceous	terrestrial
Lindsaea divaricata (x L.quadrangularis var. terrestrialminalis)	absent	membranaceous	terrestrial
Lindsaea lancea var. lancea	absent	membranaceous	terrestrial
Lindsaea ovoidea	absent	coriaceous	terrestrial
Lindsaea quadrangularis subsp.quadrangularis	absent	membranaceous	terrestrial
Lomariopsis marginata	absent	membranaceous	terrestrial
Lygodium volubile	present	membranaceous	hemiepiphyte
Megalastrum abundans	present	membranaceous	terrestrial
Megalastrum connexum	present	membranaceous	terrestrial
Megalastrum umbrinum	present	membranaceous	terrestrial
Mickelia scandens	absent	membranaceous	hemiepiphyte
Microgramma percussa	present	membranaceous	epiphyte
Microgramma squamulosa	present	coriaceous	epiphyte
Microgramma tecta	present	membranaceous	epiphyte
Microgramma vacciniifolia	poucos	membranaceous	epiphyte
Moranopterrestrialis achilleifolia	absent	coriaceous	epiphyte
Moranopterrestrialis gradata	present	membranaceous	epiphyte
Nepiphytehrolepiphyteis rivularis	present	membranaceous	terrestrial
Olfersia cervina	absent	coriaceous	terrestrial
Osmunda regalis	absent	membranaceous	terrestrial
Pecluma paradiseae	present	membranaceous	epiphyte
Pecluma recurvata	present	membranaceous	epiphyte
Pecluma truncorum	present	membranaceous	epiphyte
Pleopeltis astrolepiphyteis	present	coriaceous	epiphyte
Pleopeltis hirsutissima	present	coriaceous	epiphyte
Pleopeltis minima	present	coriaceous	epiphyte
Pleopeltis pleopeltidis	present	coriaceous	epiphyte
Polybotrya cylindrica	present	membranaceous	hemiepiphyte
Polyphlebium angustatum	absent	membranaceous	epiphyte
Polyphlebium diaphanum	absent	membranaceous	epiphyte
Polyphlebium hymenophylloides	absent	membranaceous	epiphyte
Polyphlebium pyxidiferum	present	membranaceous	epiphyte
Polypodium chnoophorum	present	membranaceous	epiphyte
Polytaenium cajenense	absent	coriaceous	epiphyte
Polytaenium lineatum	absent	coriaceous	epiphyte
Pterrestrialidium arachnoideum	present	coriaceous	terrestrial
Pterrestrialis angustata	absent	membranaceous	terrestrial
Pterrestrialis decurrens	absent	membranaceous	terrestrial
Pterrestrialis deflexa	absent	coriaceous	terrestrial
Pterrestrialis splendens	absent	coriaceous	terrestrial
Radiovittaria stipitata	absent	coriaceous	epiphyte
Rumohra adiantiformis	absent	coriaceous	epiphyte
Saccoloma brasiliense	present	membranaceous	terrestrial
Salpichlaena volubilis	present	coriaceous	hemiepiphyte
Schizaea elegans	absent	coriaceous	terrestrial
Serpocaulon catharinae	absent	coriaceous	epiphyte
Serpocaulon fraxinifolium	absent	coriaceous	epiphyte
Serpocaulon latipes	absent	coriaceous	epiphyte

Species	Indumentum	Laminar thickness	Life form
Stigmatopterrestrialis brevinervis	absent	membranaceous	terrestrial
Stigmatopterrestrialis caudata	absent	membranaceous	terrestrial
Stigmatopterrestrialis heterrestrialocarpa	absent	membranaceous	terrestrial
Tectaria incisa	absent	membranaceous	terrestrial
Thelypterrestrialis decussata	present	coriaceous	terrestrial
Thelypterrestrialis lugubris	NA	NA	terrestrial
Thelypterrestrialis maxoniana	present	membranaceous	terrestrial
Thelypterrestrialis paranaensis	present	coriaceous	terrestrial
Thelypterrestrialis tamandarei	present	membranaceous	terrestrial
Trichomanes cristatum	present	membranaceous	epiphyte
Trichomanes pilosum	present	membranaceous	epiphyte
Trichomanes polypodioides	present	membranaceous	epiphyte
Vandenboschia radicans	present	membranaceous	epiphyte
Vittaria graminifolia	absent	coriaceous	epiphyte
Vittaria lineata	absent	coriaceous	epiphyte
Vittaria scabrida	absent	coriaceous	epiphyte

Table S2. Model selection confronting idiosyncratic, neutral dynamic, niche, Emergent Groups, and Emergent Groups with ecological drift models for fern species abundances on local communities. EG=Emergent Group; L=localities; SP=species; S=sampled sites, altitude as categorical variable or A=altitude as a second order polynomial; ES=ecological strategy, which is a factor with one level for each combination of traits observed in the species; ES 01 = laminar thickness and indumentum; ES 02 = indumentum and life form; ES 03 = laminar thickness and life form; ES 04 = laminar thickness, indumentum and life form; |=conditioned to; *=interacting with.

Model	Effects	AIC	ΔAIC	df	Weight
EG with limited dispersal	ES 03 * A + 1|SP + L|SP + S|SP	19150.5	0.0	15	0.9624
EG with limited dispersal	ES 02 * A + 1|SP + L|SP + S|SP	19157.3	6.8	15	0.0316
EG with limited dispersal	ES 03 + 1|SP + L|SP + S|SP	19162.0	11.6	7	0.0030
EG with limited dispersal	ES 02 + 1|SP + L|SP + S|SP	19162.9	12.4	7	0.0019
EG with limited dispersal	ES 04 + 1|SP + L|SP + S|SP	19164.0	13.5	8	0.0011
Neutral dynamic	L|SP + S|SP	19171.9	21.4	3	<0.001
EG with limited dispersal	ES 01 + 1|SP + L|SP + S|SP	19177.5	27.0	6	<0.001
EG with limited dispersal	ES 01 * A + 1|SP + L|SP + S|SP	19177.7	27.2	12	<0.001
EG with limited dispersal	ES 04 * A + 1|SP + L|SP + S|SP	19225.8	75.3	18	<0.001
EG with limited dispersal	ES 04 * A + 1|SP + L|SP	59387.2	40236.7	17	<0.001
EG with limited dispersal	ES 03 * A + 1|SP + L|SP	59507.7	40357.3	14	<0.001
EG with limited dispersal	ES 02 * A + 1|SP + L|SP	61852.6	42702.1	14	<0.001
EG with limited dispersal	ES 01 * A + 1|SP + L|SP	64182.7	45032.2	11	<0.001
EG with limited dispersal	ES 03 + 1|SP + L|SP	67261.7	48111.2	6	<0.001
EG with limited dispersal	ES 04 + 1|SP + L|SP	67263.6	48113.1	7	<0.001
EG with limited dispersal	ES 02 + 1|SP + L|SP	67263.6	48113.2	6	<0.001
EG with limited dispersal	ES 01 + 1|SP + L|SP	67274.8	48124.3	5	<0.001
Neutral dynamic	L|SP	67318.6	48168.2	2	<0.001
EG	ES 04 * A + 1|SP	69147.2	49996.7	16	<0.001
EG	ES 03 * A + 1|SP	69267.6	50117.2	13	<0.001
EG	ES 02 * A + 1|SP	71612.4	52461.9	13	<0.001
EG	ES 01 * A + 1|SP	73939.4	54789.0	10	<0.001
Idiosyncratic	Idiosyncratic	79517.7	60367.2	3	<0.001
EG	ES 03 + 1|SP	79910.6	60760.2	5	<0.001
EG	ES 04 + 1|SP	79912.6	60762.2	6	<0.001
EG	ES 02 + 1|SP	79912.6	60762.2	5	<0.001
EG	ES 01 + 1|SP	79920.6	60770.2	4	<0.001
Niche	ES 04 * A	103844.2	84693.7	15	<0.001
Niche	ES 03 * A	104207.3	85056.8	12	<0.001
Niche	ES 02 * A	107090.4	87939.9	12	<0.001
Niche	ES 04	111721.8	92571.3	5	<0.001
Niche	ES 03	111973.9	92823.4	4	<0.001
Niche	ES 02	112606.6	93456.1	4	<0.001
Niche	ES 01 * A	114330.2	95179.8	9	<0.001
Niche	ES 01	117334.8	98184.3	3	<0.001

Table S3. Summary statistics for the best model that includes ecological strategy interacting with altitude as fixed effects and drift and limited dispersal as random effects. Formula: abundance $\sim$ life form $*$ altitude $+$ life form $*$ altitude^2 $+$ laminar thickness $*$ altitude $+$ laminar thickness $*$ altitude^2 $+$ (1 | species) $+$ (1| locality:species) $+$ (1|sampled site:species).

Fixed Effect	Estimate	Standard error
Intercept	-8.42	0.59
hemiepiphyte	4.22	1.99
epiphyte	0.66	0.56
altitude	2.31	3.07
altitude^2	-3.41	3.29
membraneceous	-0.56	0.56
hemiepiphyte:altitude	12.27	10.52
epiphyte:altitude	-5.58	3.18
hemiepiphyte:altitude^2	-15.14	10.40
epiphyte:altitude^2	7.87	3.41
altitude:membraneceous	7.77	3.12
altitude^2:membraneceous	-7.77	3.30
Random Effect	**Variance**	**Standard deviation**
sampled sites:species	44.990	6.707
locality:species	4.475	2.115
species	0.000	0.000

3 — Padrões e processos filogenéticos

Can phylogenetic structure reveal local niche and neutral processes in community assembly?

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Abstract

Community phylogeny approach restarted the discussion of community assembly rules in community ecology and the related question of how can we infer processes shaping commnunities from patterns. The basic idea is that species relatedness in local communities, represented by a measure of phylogenetic diversity, reflect whether communities are structured by competition or environmental filter. One aspect overlooked in this approach is wheter processes not based on niche differences, such as neutral processes, could affect the outcome of phylogenetic structure. Since it is recognized that communities are a result of both niche and neutral processes, our main question is can phylogenetic structure determine the relative role of niche and neutral processes in community assembly? Based on observed data of fern communities on elevational gradients we built statistical models to simulate communities built by purely niche process (e.g., environmental filters), purely neutral processes (drift and limited dispersal), and both acting together. We hypothesize that as we increase the influence of neutrality, the probability of detecting a non-random phylogenetic structure decreases. Our results show that a non-random phylogenetic strucutre can emerge from niche processes but in our dataset occurred is a very low proporion. In addition, it is unlikely to occur when niche and neutral processes occur together or when communities are driven only by neutrality. Therefore, we cannot distinguish based on community patterns which communities are built by niche or neutral processes. This result highlights the importance of drift and limited dispersal in determining the phylogenetic structure of local communities. In conclusion, since a random pattern is typical of all simulated

communities, in scenarios involving a mix of niche and neutral processes phylogenetic structure does not have the ability to disentangle those processes.

3.1 Introduction

In community assembly theory (WEIHER & KEDDY 1999), major processes that limit the regional pool to drive community assembly are dispersal limitation and environmental filtering (CAVENDER-BARES et al. 2009; HILLERISLAMBERS et al. 2012). Thus, species composition and abundances in local communities would reflect the combined effects of primarily these processes. Similarly, there is a growing understanding that both neutral and niche processes affect community assembly (CONNOR & SIMBERLOFF 1979; TILMAN 2004; GRAVEL et al. 2006; ADLER, HILLERISLAMBERS & LEVINE 2007; VELLEND et al. 2014). Therefore, when neutral processes prevail the importance of dispersal limitation would be higher, whereas if niche processes prevail the most important mechanisms would be abiotic or biotic filters. Core ideas of how dispersal, environmental and biotic filtering can affect community assembly comes from assembly rules (DIAMOND 1975; KEDDY 1990; WEIHER & KEDDY 1999). Ranging from its first proposal by DIAMOND (1975), in which he attempted to identify a subset of co-occurring species based on competitive interactions, to later attempts to identify a subset of traits shared by co-occurring species (WEIHER & KEDDY 1995), community assembly rules are a set of constrains that predict species, traits or guilds in a given community (WEIHER & KEDDY 1995). Community assembly theory received renewed attention after Chesson's (2000) modern coexistence theory and Webb et al's (2002) ideas of community phylogenetic structure, bringing back to discussion Darwin's competition-relatedness hypothesis (HILLERISLAMBERS et al. 2012; GODOY, KRAFT & LEVINE 2014) which states that closely related species are not likely to coexist in local communities.

Community phylogenetic structure approach brought back the discussion of community assembly rules (DIAMOND 1975; WEIHER & KEDDY 1999) in community ecology. As many other observational approaches this also brought the question of whether we can infer processes shaping communities from patterns (HILLERISLAMBERS et al. 2012; GODOY, KRAFT & LEVINE 2014). The idea of using a verbal model of trait dispersal to infer processes shaping communities invoked by community phylogenetics and hereafter described comes from the assembly rule literature (WEIHER & KEDDY 1995). WEBB et al. (2002) then added phylogenetic relatedness of species to look at trait dispersal patterns. Community phylogenetic structure approach purports to be a means of separating the effects of competitive exclusion and environmental filtering in shaping local communities. Specially because of limiting similarity closely related species sharing similar traits would not coexist in local communities resulting in a phylogenetic overdispersed pattern. However, a phylogenetic overdispersed pattern can be a result of environmental filtering selecting distant related species sharing similar traits. Environmental filtering generates a phylogenetic clustered pattern if the environment is selecting closely related species sharing similar traits near the optimum for that environment.

The idea of a clear link between pattern and processes through community phylogenetics became widespread in community ecology since the entire conceptual framework (WEBB et al. 2002; KRAFT et al. 2007; CAVENDER-BARES et al. 2009) and statistical tools (WEBB, ACKERLY & KEMBEL 2008; KEMBEL et al. 2010) became easily available to community ecologists [1]. Even though community phylogenetic was widely applied in community ecology to infer processes from patterns as a simple pattern test, we often find misleading empirical results (VAMOSI et al. 2009; MAYFIELD & LEVINE 2010). For instance, trait clustering, generally understood as a result of environmental filtering, can also be generated by competition (CAVENDER-BARES et al. 2009; MAYFIELD & LEVINE 2010). Random phylogenetic structure can be found when competition and environmental filtering occur together and obscure one another (HELMUS et al. 2007). CAVENDER-BARES et al. (2009) shed light on how different processes occurring together can result on the patterns proposed by WEBB et al. (2002). The idea in community phylogenetics was extended with the notion that since the importance of competition and filtering varies from a small to a larger scale respectively, the outcome in terms of phylogenetic structure can vary by scale as well (SWENSON et al. 2006; CAVENDER-BARES et al. 2009). For instance, it is expected that density-dependent interactions will be stronger in a neighbourhood scale, environmental filtering on a habitat scale and biogeographical processes (WIENS & DONOGHUE 2004) at larger spatial scales (SWENSON et al. 2006; CAVENDER-BARES et al. 2009). There is empirical evidence that phylogenetic clustering can increase from local to regional spatial scales (CAVENDER-BARES et al. 2009; SWENSON et al. 2006; SWENSON et al. 2007) following the influence of different processes changing with scale so that biogeographical processes and limited dispersal can lead to a clustered phylogenetic pattern (WIENS & DONOGHUE 2004). Therefore, attempting to predict what how dispersal affects community phylogenetic strucutre. These models are all verbal models, leaving a rigorous simulation-based analysis of the role of limited dispersal and other neutral processes on phylogenetic local patterns still to be explored (HARDY 2008; KEMBEL 2009).

Understanding links – or the lack of links – between pattern and processes in community phylogenetics requires clarifying basic assumptions underlying the phylogenetic community approach (MAYFIELD & LEVINE 2010). The first assumption is that detecting a phylogenetic structure in community assembly requires traits to be phylogenetically conserved or to have phylogenetic signal so that phylogenetic distance is related to distance in phenotype space. Second, phylogenetic structure of a community must reflect local interactions rather than just be an echo of regional processes carried into local communities. Third, competitive exclusion or environmental filtering must dominate assembly processes, otherwise it would be difficult to identify and therefore separate their effects. Violation of one or more of these assumptions makes inference about processes based on phylogenetic patterns weak (MAYFIELD & LEVINE 2010). Thus, we need ways to test these assumptions to before we can hope to infer process from patterns in community phylogenetics. The assumption that competitive exclusion or environmental filtering dominates assembly processes brings up an important issue that is usually neglected in

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[1]The fast spread of an idea and methods also occurred with assembly rules after the increase in computational power and null models development from GOTELLI & GRAVES (1996)

community phylogenetics approach: how the detection of a non-random phylogenetic structure is influenced by neutral processes or by neutral and niche processes operating together. The simplest prediction from the influence of neutral processes affecting phylogenetic structure would be that neutral processes generate a random phylogenetic structure. Indeed, from classic assembly rules theory, a random trait dispersal would be due to historical contingency. However, since both neutral and niche processes can jointly affect local communities, it is important to recognize what phylogenetic structure would emerge from the combination of both. The basic prediction would be that neutrality adds noise to the detection of non-random structure affecting its intensity but not the signal. But this hypothesis remains untested (HARDY 2008; VAMOSI et al. 2009).

Our goal is to rigorously explore using simulation how phylogenetic structure patterns vary if neutral processes also matter to community assembly. We tested how frequent is the detection of a non-random phylogenetic structure in communities built solely by niche, solely by neutrality or a combination of both processes. Our prediction is that as we add the influence of neutral processes the detection of a non-random phylogenetic structure would decrease. We used linear models to describe the variation of abundance of species across altitudes in three regions as the outcome of niche and neutral processes. We then simulated communities with real-world parameter values for niche, neutral and combination of both scenarios based on data of fern metacommunities across altitudinal gradients. Because we aimed to have realistic estimates of niche and neutral parameters we performed stochastic simulations instead of dynamic simulations.

3.2 Methods

3.2.1 Fern communities, traits and phylogeny

We used data from a fern metacommunity on altitudinal gradients in the Atlantic Rainforest, Brazil to provide real-world parameters used to generate communities based on different processes. The data we used to parametrize the simulations were collected by PACIENCIA (2008) in three different mountain ranges, all occurring at the same region. At each mountain ten 20 x 20 m plots were placed across an altitudinal gradient ranging from 0 to 1400 m a.s.l.. From each plot we have data of species abundance and richness. PACIENCIA (2008) recorded 19,884 individuals from a pool of 155 species at 30 sampling sites.

In our previous work we identified an association of species traits and abundance. Using a novel method based on linear mixed models (Chapter 2), we found that species abundances are a result of a mixture of environmental filtering and also drift and limited dispersal. Thus this empirical system represents a good test system for what happens when both neutral and niche (filter) dynamics cooccur. The traits that mediate the environmental filtering processes were laminar thickness, indumentum and life form. Laminar thickness represents the potential of a species to store water and deal with water limitation conditions, here defined as thin (from membranaceous to papipaceous leaves) or thick (from cartaceous to coriaceous leaves). Presence of an indumentum represents a strategy to reduce water loss from evapotranspiration, here categorized as presence or absence. Life form is defined based on the habitat that a species

occupies, being: terrestrial, hemiepiphye or epiphyte.

In order to calculate the phylogenetic structure measure we used a phylogeny of these species of ferns based on LEHTONEN (2011) to infer the phylogenetic distance among species in each local community. Since the first MAYFIELD & LEVINE (2010) assumption is that traits involved in community assembly must have phylogenetic signal, we tested for the signal of all traits on the phylogeny and we found a significant phylogenetic signal for laminar thickness and life form but no signal for indumentum. Nevertheless we used the three traits in our simulations to emulate a realistic scenario of partial fulfillment of the assumptioms.

3.2.2 Simulation of niche, neutral, and niche and neutral communities

In our previous work we developed a generalized liner mixed model (GLMM) that fits very well to the data with different coefficients that measure the relative contribution of niche (environmental filtering) and neutrality (drift and limited dispersal). We used a Poisson GLMM to model abundance of each species in each sampling site. In the GLMM, environmental filtering was described by fixed effects and drift and limited dispersal by random effects. To implement a combined niche and neutral model, we followed the HERAULT 2007 approach which uses a hierarchy – niche differentiation occurs between groups of species with shared traits and neutrality occurs as random variation in abundances among species within a group. Thus, the niche component of the model predicts mean abundance of species sharing a particular combination of traits. Within species sharing the same combination of traits variation in abundance is attributed to random variation across species (the drift component) and to random variation of species across sites (the limited dispersal component). These GLMM models can be fit to empirical data to estimate the parameters for deterministic niche-based abundance expected by traits as well as random variance of the expected abundances due to neutral processes within a group of species sharing the same traits. The fitted model can then be used to simulate expected abundances of each species, giving the variance caused by random effects. Moreover, we can simulate communities built by purely niche effects or by niche and neutral effectsby keeping only fixed or random effects in the calculation of predicted values. Within this modeling framework we performed parametric simulations of communities affected by: (i) only environmental filtering, (ii) environmental filtering with drift and limited dispersal, and (iii) only limited dispersal as hereafter described.

For the first and second scenarios – environmental filtering and environmental filtering with drift and limited dispersal – we performed the simulations based on the parameters for a Poisson GLMM that best fit to the data (Table 3.1) [2]. In the case of the scenario with only drift and limited dispersal we performed the simulations with the model with the best random structure, which is the same as in the best model, without the fixed effects. In the first scenario, we simulated new abundance values for each species only from the fixed effects from the best model. This is the scenario in which communities are built only by environmental filtering,

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[2]For this Chapter we have chosen the best model that fits the data that has strictly niche processes represented by fixed effects, and neutral processes represented by random effects. For generating the communities we used either, fixed, random or both effects.

represented by the effect of species traits mediated by elevation. We performed the simulation
by sampling species abundance at each local community from Poisson distributions with the
expected values predicted by fixed effects. The second scenario was done based on fixed and
random effects. This is the scenario in which communities are built by environmental filtering,
drift, and limited dispersal, meaning that the expected abundances for for each trait have a
random variance component among species and among mountain ranges. We performed the
simulation by generating new expected abundances for each species from a normal distribution
with the mean equal to fixed effects and the standard deviation equal to the standard deviation
estimated for random effects. Finally, in the third scenario we simulated data only from random
effects. In this scenario, communities are built only by neutral processes as drift under limited
dispersal, restricted to the different mountains. We performed the simulation by simulating new
expected abundances for each species at each local community for all of random effects. For
each scenario described above we simulated 1,000 communities using the functions of the R
package `lme4` (BATES et al. 2015) `predict` to calculate the expected values for Poisson samples
used in the 1st scenario (fixed effects) and `simulate` to simulate abundances for the 2nd and 3rd
scenario (random and random + fixed effects). .

Table 3.1: Models, effects and simulation procedure for each simulated scenario. ES=ecological
strategy; A=altitude as a second order polynomial; SP=species; L=localities; ∗=interacting with;
|=conditioned to. See Supplementary material Tables S1 and S2 for parameters of the models
used on the simulations.

Scenario	Model	Simulated effects		Simulation procedure
		Fixed	**Random**	
■ Environmental filtering	Best model adjusted to data	ES∗A		Sampling from predicted values by fixed effects (`predict` function)
■ Environmental filtering with drift and limited dispersal	Best model adjusted to data	ES∗A	1|SP + L|SP	Simulating new values for all fixed and random effects (`simulate` function)
■ Drift and limited dispersal	Model with the best random structure		1|SP + L+SP	Simulating new values for all random effects (`simulate` function)

3.2.3 Statistical analysis

Phylogenetic structure

For each simulated community in all scenarios we calculated the Mean Phylogenetic Distance
(MPD) to represent the phylogenetic structure for each community. In order to obtain the amount
of non-random phylogenetic structure from each scenario, we compared each MPD value with

the distribution of the values from null scenarios. The null scenarios were generated by random permutation of species abundances across sites using the swap algorithm (GOTELLI 2000). Then, in order to compare the values of MPD from simulated communities with the null expectations we used the standardized MPD (sesMPD; the net relatedness index NRI) (WEBB 2000; WEBB et al. 2002), as follows:

$$sesMPD = -\ \frac{MPD_{observed} - MPD_{random}}{sd(MPD_{random})}$$

Standardized MPD values > 1.96 represent significantly clustered communities whereas sesMPD < -1.96 represent significantly overdispersed communities. Finally, we calculated the proportion of non-random phylogenetic structure in each one of the six scenarios as the amount of MPD values > 1.96 or < -1.96. We calculated the MPD, sesMPD with the swap null model using the `ses.mpd` function on R from `picante` package (KEMBEL et al. 2010).

Phylogenetic structure across the altitudinal gradient

Since the data we used to parametrize the communities comes from communities across an altitudinal gradient, we aimed to explore the relation of sesMPD to the altitudinal gradient for each simulated scenario. In order to understand the relation of sesMPD with the altitudinal gradient we tested whether sesMPD had a monotonic or non-monotonic response to altitude on linear Gaussian regressions with sesMPD as response variable. We compared models with altitude as a linear function and as a quadratic function, with the additive and interactive effects of altitude and richness. We included richness in the models because there is a response of richness to the altitudinal gradient (Figure S1) that covaries with sesMPD. The models were compared using the Akaike Information Criteria (AIC). The model with lowest AIC value was selected as the most plausible and models with ΔAIC < 2 were considered equally plausible. Model fit and comparison were done on R software (R CORE TEAM 2015).

3.3 Results

3.3.1 Patterns of phylogenetic structure

We found that only a small proportion of non-random phylogenetic structure occurred in communities built solely by filtering (0.077±0.013 SE). Detection of a non-random phylogenetic structure decreased considerably more as we added the influence of neutral processes on community assembly. As a result, there is no distinction in terms of phylogenetic structure between communities built by filtering and neutrality (0.001±0.0001 SE) and those built solely by neutrality (0.001±0.0002 SE).

In the scenario in which communities are built solely by filtering processes, the proportion of non-random phylogenetic structure across the altitudinal gradient showed a shift on 800 m from clustered to overdispersed communities (Figure S2a). For this purely niche scenario, clustering at low altitudes is related with filtering processes selecting few species from a few clades such as the genus *Blechnum*, *Campyloneurum*, and *Ceradenia* (the latter two from the same clade; Figure S3a). On the other hand, overdispersal at high altitudes is related with

filtering processes selecting several species from different clades across the phylogeny (Figure S3b). In this case, species are aggregated in clades (such as the clade *Actinostachys* and *Schizaea*, and the genus *Arachnoides*, *Blechnum*, *Cyathea*, *Danea*, *CDoryopteris*, *Ceradenia*, *Lindsaea*, *Polybotrya*, *Pteris*, and *Thelypteris*), but filtered clades are spread across the phylogeny. For the scenarios in which we added the influence of neutral processes there was a constant low detection of non-random phylogenetic structure across the altitudinal gradient (Figure S2b-c). Again, there is no difference between the scenarios in which filtering and neutral processes operate together and the solely neutral scenario.
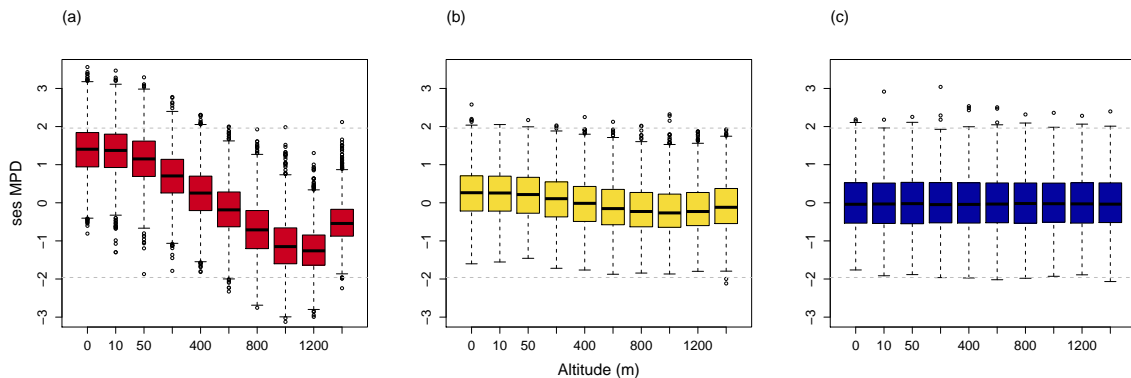

Figure 3.1: Standardized MPD for each scenario. (a) communities built by filtering; (b) communities built by filtering and neutrality; (c) communities built by neutrality processes. Values above the top dashed gray line are significantly clustered and values under the bottom dashed gray line are significantly overdispersed.

3.3.2 Responses of phylogenetic structure to richness and the altitudinal gradient

The shift from clustered to oversdispersed communities on simulations built by environmental filtering, can be seen in terms of the decay of sesMPD along the altitudinal gradient (Figure 3.1). In the purely niche scenario, we found that sesMPD has a quadratic response to the altitude interacting with richness (for model selection table and model coefficients see Table S3 and S6). At lower altitudes, the phylogenetic structure of communities built by environmental filters can be significantly clustered specially in communities with less species (Figure 3.2a-c). At extreme high altitudes the phylogenetic structure can be overdispersed in communities with a higher number of species (Figure 3.2g-j). Sites at intermediate altitudes exhibited a random phylogenetic structure and less species than communities on extreme high altitudes (Figure 3.2d-f). For communities built by filtering and neutrality sesMPD shows a quadratic response to the environmental gradient (Table S4 and S7) but there was no distinction between the model with and without richness. In contrast, communities built solely by neutrality show no response to the altitudinal gradient, however there was no distinction between the constant and the richness models (Table S5 and S8).
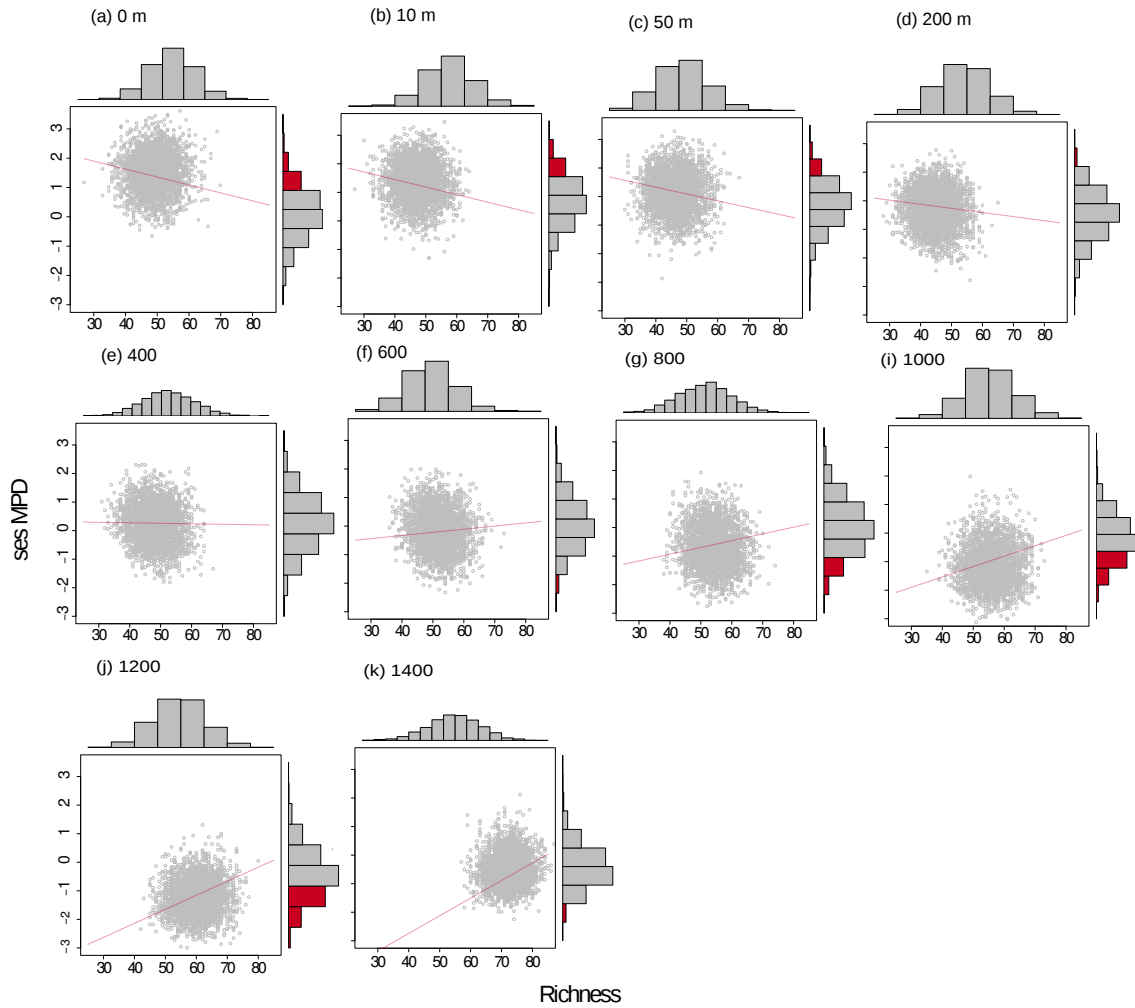
Figure 3.2: Standardized MPD and richness values for each local community built by environmental filtering processes. The red lines represent the fit of the sesMPD ∼ richness + altitude + richness*altitude linear model at each altitude. Red bars on the histograms represent non-random sesMPD values.

3.4 Discussion

3.4.1 Linking pattern and processes

Based on our stochastic simulations of communities, we showed that communities built by niche processes can exhibit a non-random phylogenetic structure, but do so rarely. We also show how random variation in abundances can blur any signal of phylogenetic structure, making the results of joint neutral and niche processes indistinguishable from that of purely neutral processes. According to MAYFIELD & LEVINE (2010) the phylogenetic diversity approach in community ecology should follow basic assumptions. Hereafter, we use these three assumptions to discuss the results of our empirical system. First, traits must have phylogenetic signal and from the three traits that mediated the filtering mechanism, only life form and laminar thickness present a phylogenetic signal while indumentum does not. According to model parameters we used to generate the commmunities based on niche processes, coefficients expressing laminar thickness

are among the largest and all coefficients expressing the interaction of traits with altitude present high values (See Table S1). High values of model coefficients express how traits are strongly affecting species abundance. Laminar thickness is a trait that exhibit a weak phylogenetic signal, and together with the high importance of interactions of species traits with altitude it may suggest that at some altitudes traits with a weak phylogenetic signal are more important. This may be responsible for the low detection of a non-random phylogenetic structure in communities built only by niche. Second, either competition or environmental filter must dominate. Indeed, when communities are build based only on filtering process the pattern of a non-random phylogenetic structure emerges but it is very unlikely. Therefore, even in the scenario where environmental filter is the only process affecting species abundance, we do not detect a non-random pattern of phylogenetic structure as expected by the community phylogenetic framework. Finally, the third assumption is that local interactions should shape the phylogenetic structure. Local filtering does generate a weakly non-random phylogenetic patterns, but combining this with local drift processes eliminates the non-random nature. MAYFIELD & LEVINE (2010) suggest that violation of one of these assumptions results in a weak link between pattern and processes. In our case study, even with traits with phylogenetic signal and environmental filtering dominating, a non-random pattern of phylogenetic structure is not commonly seen. In addition, the result from the niche and neutral scenario shows that the effect of local interactions on phylogenetic structure are blurred by the influence of regional limited dispersal.

Our work shows that a non-random phylogenetic structure is unlikely to be found in all the simulated scenarios. Moreover, even when only environmental filtering is used to simulate species abundances, phylogenetic structure is not a common outcome, and seems restricted to the extremities of the environmental gradient. However, VAMOSI et al. (2009) reviewed 24 papers that assess phylogenetic structure of communities and showed that only 6 of 39 cases showed a random phylogenetic strucure. There are two reasons for the contrasting results we found and VAMOSI et al. (2009) reported. First, there may be a publication bias favoring the publication of papers that detect a non-random phylogenetic structure. Second, SILVERTOWN et al. (2006) propose a conceptual model of how niche structured communities can exhibit a random phylogenetic pattern. Hierarchical filtering (SILVERTOWN et al. 2006) can result in niche conservatism of species pool and local labile traits. Thus, hierarchical filtering of species on community assembly may be a general mechanism resulting in the lack of ecological and evolutionary links on local communities (SILVERTOWN et al. 2006). For fern communities across elevational gradients, KLUGE & KESSLER (2011) showed that local communities exhibited a predominantly random phylogenetic structure along the gradient and they attributed the result to the lack of relationship of trait and phylogenetic diversity. Therefore, trait selection on local communities might occur independent of species phylogeny which does not mean that a random phylogenetic pattern is independent of niche processes. Indeed, what our case study shows is that some of the traits that are mediating filtering processes exhibit a weak or no phylogenetic signal. However those traits are still strongly affecting species abundance. Therefore, the influence of niche processes on community assembly may not always result in a non-random pattern of phylogenetic structure as shown by SILVERTOWN et al. (2006) and KLUGE & KESSLER (2011).

Based on the outcome of the purely neutral scenario, we have evidence that drift and limited dispersal clearly generate phylogenetic random patterns. However, when drift and limited dispersal occur together with environmental filtering, we still see a random phylogenetic pattern, showing that random variation of abundance – attributed to neutral processes – can easily obscure the pattern of phylogenetic structure. KEMBEL (2009) suggested that dispersal could have an important effect on community phylogenetic structure. Our case study empirically shows that when dispersal affects community assembly, neutral processes seem to prevail on determining the outcome of phylogenetic structure. In this era of assessing the relative importance of niche and neutral processes on community assembly, it is an important step to identify that when niche and neutral processes operate together, the signature of neutral processes seems to prevail at least in phylogenetic structure.

3.4.2 Relashionship of phylogenetic structure, richness and the altitudinal gradient

Regardless of the low detection of a non-random phylogenetic structure on the purely niche scenario, we do see a unimodal response of the phylogenetic structure across the altitudinal gradient, mediated by local richness. It is worth noting that whereas in niche based communities phylogenetic structure shows a response to the altitudinal gradient, in the other scenarios increasing amounts of neutrality reduces the variability of phylogenetic structure across the altitudinal gradient. For the niche scenario we observed that the detection of a non-random phylogenetic structure is more pronounced on the extremes of the gradient, while on intermediate portions of the altitudinal gradient we see a random phylogenetic structure. At low altitudes, clustering occurs where there is a low number or cooccurring species. Conversely, at high altitudes, overdispersal occurs where communities exhibit a high number of species. It is important to consider that variation in local richness on purely niche simulations is only due to the sampling process of species abundance from a Poisson distribution. Therefore, the increase on local richness occurs when we sample species with low probabilities of occurrence. The increase of species with low occurrence probabilities above 200 m obscures the aggregated pattern of lower altitudes, resulting in random patterns. Conversely, above 600 m, the increase of species with low occurrence probabilities results in an overdispersed pattern where different groups across the phylogeny are being selected by environmental filtering. The unimodal pattern across the altitudinal gradient suggests that the strength of biotic and abiotic filters on extremes of the gradient is stronger than on intermediate altitudes. The random phylogenetic pattern on intermediate altitudes of the altitudinal gradient suggests that intermediate altitudes, where there is more humidity, are unlikely to act as an environmental filtering (KLUGE & KESSLER 2011). Moreover, it is unexpected to see an overdispersed phylogenetic structure in this scenario since the traits are conserved and the underlying process is environmental filtering. It seems that different tradoffs of each trait with altitude resulted in few cases conforming to expectations for limiting similarity.

3.4.3 Concluding remarks on pattern and processes

Even though we showed that communities built by environmental filtering can exhibit a non-random phylogenetic structure the frequency in which that happens is very low. We created a scenario that is relatively simple, where local communities are generated by the tradeoff of three distinct traits with the environment. However, the three traits have different degrees of phylogenetic signal, resulting in a low detection of non-random phylogenetic structure. If even in a simple simulation we have low detection of non-random phylogenetic structure, it seems likely that in the real world there is a very low probability of detection. This conclusion is further enhanced because we found clearly that even in combination with niche processes, drift and limited dispersal drastically reduced the likelihood of finding a non-random phylogenetic structure. The framework we present on Chapter 2 indicates that most of the variation of species abundance are not being explained by species traits. The role of stochastic variation on species abundance seem to prevail, and therefore, affect the outcome of phylogenetic structure. What deserves further investigation is how much of empirical abundance of species on different communities are due to stochastic or deterministic processes.

Our simple simulations suggest that detection in the real world of non-random phylogenetic structure is unlikely and that any non-random structure is unlikely to be indicative of what the underlying processes are. Therefore, the weak link between pattern and processes that emerged from our results highlights that the framework from community phylogenetics is not always sufficient to determine the mechanisms causing the patterns. WEIHER & KEDDY (1999) argue that in order to find assembly rules one needs to describe patterns of an assemblage, state rules that predict the pattern and, finally, determine the processes causing patterns. In community phylogenetics, the analytical procedure is well developed (KEMBEL 2009; VAMOSI et al. 2009) and the quality of phylogeny estimation has been improved in the past decades. The flaws of community phylogenetics approach in our test seem to be because the measure of phylogenetic structure ends not being informative enough to state rules and, therefore, determine the processes. In our case the phylogenetic structure is informative only in terms of its relationship with the gradient, where we see that communities with some influence of niche processes present a response to the altitudinal gradient. However, only looking at the phylogenetic structure on local communities one cannot easily distinguish the different scenarios we simulated (Figure 3.3a). Differences on local patterns among communities built by niche, neutral or both processes are not evident if we look to the pattern of phylogenetic structure and seem to be more pronounced on local richness patterns (Figure 3.3b). Local richness exhibit a similar response of phylogenetic structure to the gradient, in which communities influenced by niche processes richness covary with the altitudinal gradient. Still, similarly to the pattern of phylogenetic structure, when neutrality also affects community assembly, values of richness across the gradient are indistinguishable. In summary, when there is niche affecting the communities, both richness and phylogenetic structure patterns respond to the gradient. When there is neutrality affecting communities, communities entirely or partially influenced by neutrality are hard to tease apart. As emerged from our results, the response of phylogenetic structure to the gradient is in part driven by richness yet the pattern of richness by itself is not fully informative of processes

generating communities. One question that emerges is if we know the processes that are affecting communities, is there such a pattern that reflects underlying processes? Maybe in the vastness of patterns in community ecology we shouldn't rely on just one pattern to do all the pattern-process link. If we are capable of defining how different classes of processes affect communities, we should be able to reconstruct what are the processes that better reflect them.

Figure 3.3: General relationships of pattens of phylogenetic structure and local richness to the altitudinal gradient for each simulated scenario. Communities built by niche processes show a response of phylogenetic structure and richness to the gradient. Communities built by neutral processes exhibit local patterns independent of the gradient. In communities where both niche and neutral processes operate, there is a weak response to the gradient. Differences on local patterns among communities built by different processes are more evident on richness patterns.
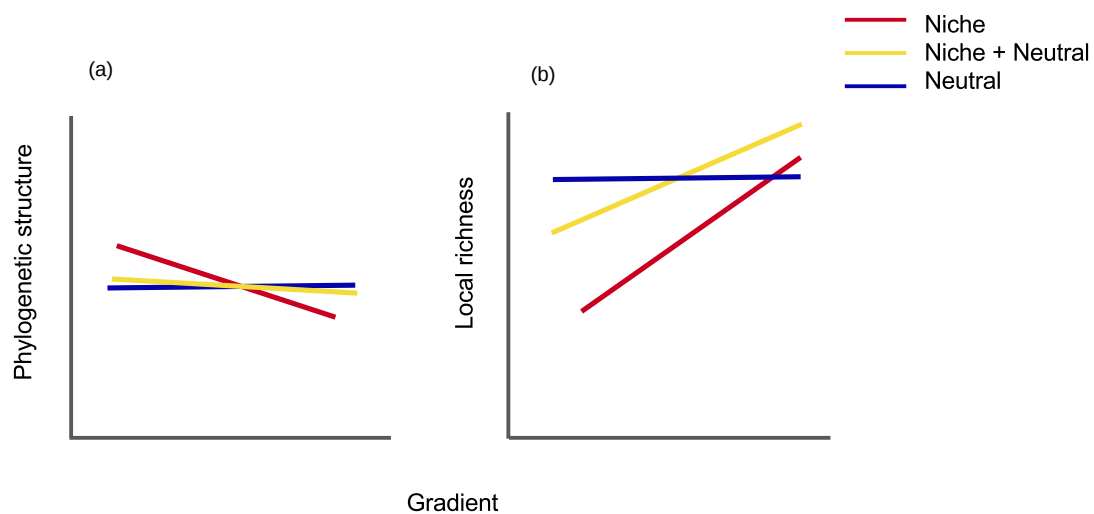

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Supplementary material

Figure S1. Local species richness across the altitudinal gradient for each simulated scenario. (a) communities built by filtering; (b) communities built by filtering and neutrality; (c) communities built by neutrality.
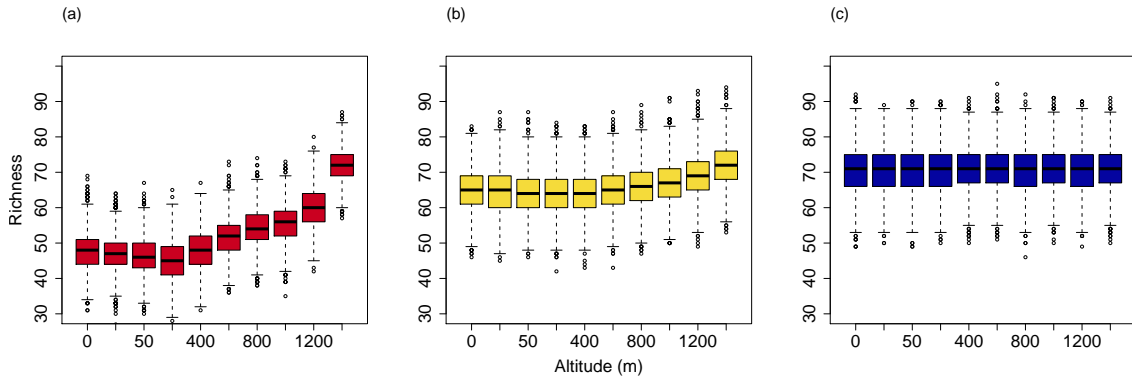

Figure S2. Proportion of non-random phylogenetic structure detected in each simulated scenario across the altitudinal gradient. (a) communities built by filtering; (b) communities built by filtering and neutrality; (c) communities built by neutrality.
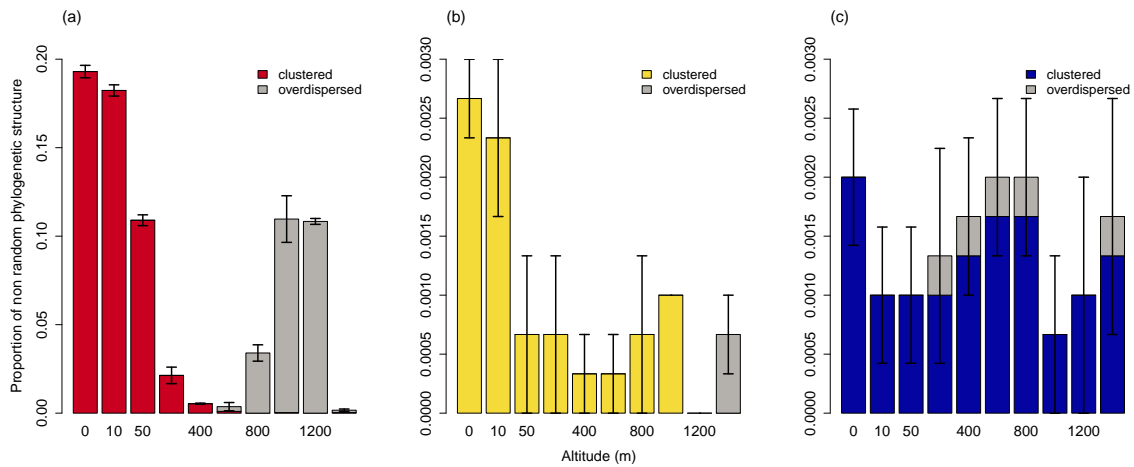
Figure S3. Phylogenetic signal Blomberg's K (BLOMBERG, GARLAND & IVES 2003) of species mean abundance across altitudes on (a) 0 m a.s.l. and (b) 1200 m a.s.l. We calculated the phylogenetic signal for species abundance predicted by the environmental filtering effects.
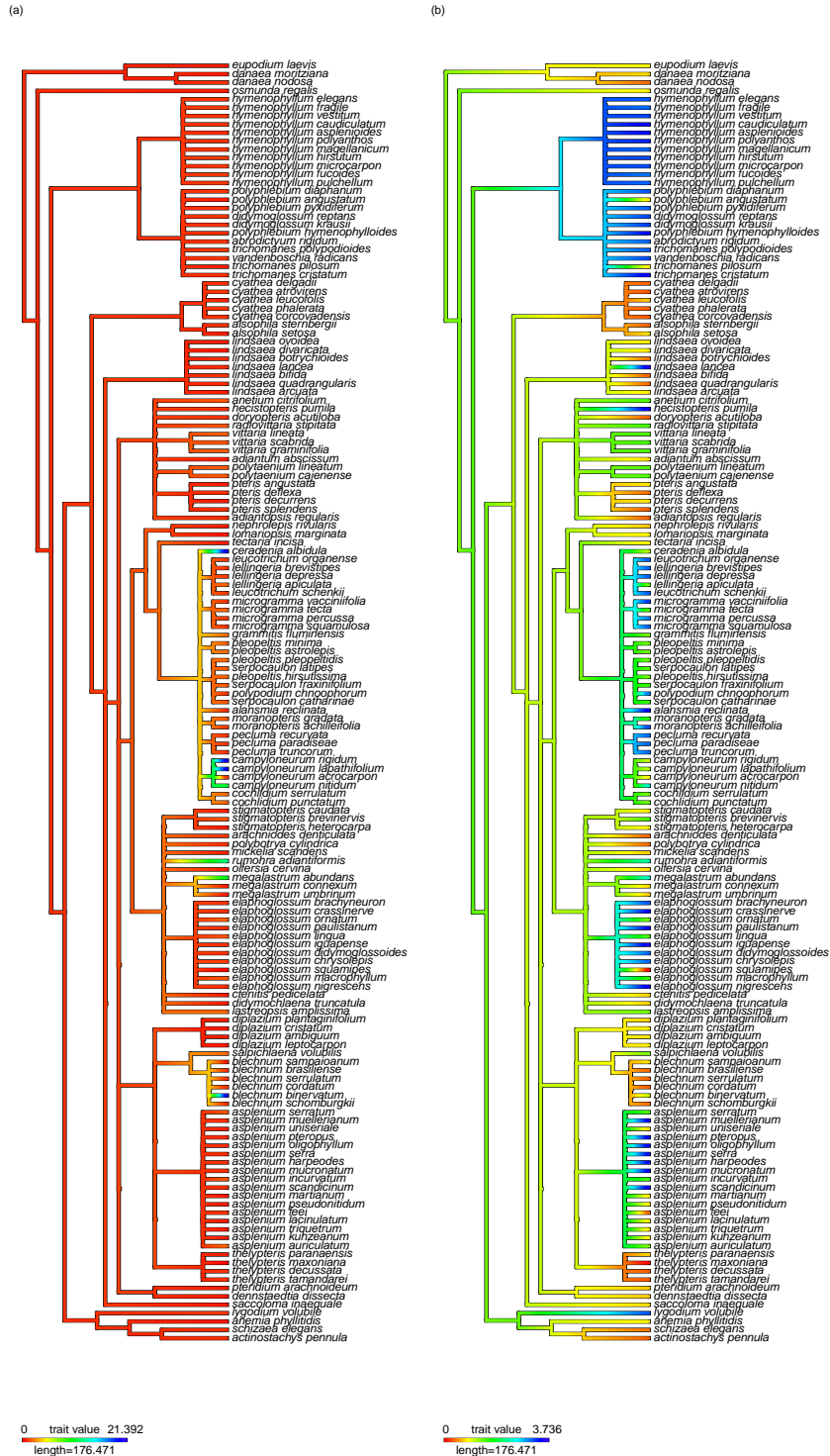
Table S1. Parameter estimates of models used to simulate the purely niche and niche and neutral scenarios. Formula for best niche and neutral model: abundance $\sim$ life form $*$ altitude $+$ life form $*$ altitude^2 $+$ laminar thickness $*$ altitude $+$ laminar thickness $*$ altitude^2 $+$ indumentum $*$ altitude $+$ indumentum $*$ altitude^2 $+$ (1 | species) $+$ (1|localities:species).

Fixed effect	Estimate	Standard error
(Intercept)	-1.1794	0.3293
hemiepiphyte	3.1404	0.7518
epiphyte	0.6454	0.3252
altitude	-2.6799	0.1882
Altitude^2	1.8173	0.1996
indumentum present	0.1586	0.3206
membranaceous	-0.6594	0.3227
hemiepiphyte:altitude	0.8274	0.2742
epiphyte:altitude	-4.6396	0.1928
hemiepiphyte:altitude^2	-3.6725	0.3505
epiphyte:altitude^2	6.5256	0.1994
altitude:indumentum present	-1.8216	0.162
altitude^2:indumentum present	1.7652	0.1608
altitude:membranaceous	9.0195	0.1936
altitude^2:membranaceous	-8.46	0.1944
Random effect	**Variance**	**Standard deviation**
locality:species	4.062	2.015
species	2.081	1.443

Table S2. Parameter estimates of the model used to simulate the purely neutral scenario. Formula for model with the best random structure: abundance $\sim$ 1 $+$ (1 | species) $+$ (1|localities:species).

Fixed effect	Estimate	Standard error
(Intercept)	-0.7684	0.1643
Random effect	**Variance**	**Standard deviation**
locality:species	4.059	2.015
species	2.478	1.574

Table S3. Model selection to test the response of sesMPD to the altitudinal gradient for communities built by environmental filtering.

	AIC	ΔAIC	df	weight
constant	93852.29	33235.53	2	0.00
altitude	68450.56	7833.80	3	0.00
altitude+altitude^2	62372.23	1755.47	4	0.00
richness	63016.22	2399.46	3	0.00
richness+altitude	66956.29	6339.53	4	0.00
richness*altitude	62627.46	2010.69	5	0.00
richness+altitude+altitude^2	62343.47	1726.70	5	0.00
richness*altitude+richness*altitude^2	**60616.76**	**0.00**	**7**	**1.00**

Table S4. Model selection to test the response of sesMPD to the altitudinal gradient for communities built by environmental filtering, drift and limited dispersal.

	AIC	ΔAIC	df	weight
constant	57999.12	2153.63	2	0.00
altitude	56434.92	589.42	3	0.00
altitude+altitude^2	**55845.81**	**0.32**	**4**	**0.39**
richness	57914.26	2068.77	3	0.00
richness+altitude	56411.40	565.91	4	0.00
richness*altitude	56352.89	507.40	5	0.00
richness+altitude+altitude^2	55847.68	2.19	5	0.15
richness*altitude+richness*altitude^2	**55845.49**	**0.00**	**7**	**0.46**

Table S5. Model selection to test the response of sesMPD to the altitudinal gradient for communities built by drift and limited dispersal.

	AIC	ΔAIC	df	weight
constant	**63015.78**	**0.00**	**2**	**0.30**
altitude	63017.06	1.28	3	0.16
altitude+altitude^2	63019.06	3.28	4	0.06
richness	**63016.22**	**0.45**	**3**	**0.24**
richness+altitude	63017.51	1.73	4	0.13
richness*altitude	63018.88	3.10	5	0.06
richness+altitude+altitude^2	63019.51	3.73	5	0.05
richness*altitude+richness*altitude^2	63022.88	7.10	7	0.01

Table S6. Model coefficients of the best model for sesMPD on communities built by environmental filtering.

	Estimate	Std. Error	t value	Pr($>$|t|)
(Intercept)	1.0695	0.0599	17.86	0.0000
richness	0.0059	0.0013	4.65	0.0000
altitude	2.2072	0.3039	7.26	0.0000
I(altitude^2)	-6.8795	0.2873	-23.94	0.0000
richness:altitude	-0.1334	0.0059	-22.47	0.0000
richness:I(altitude^2)	0.1693	0.0053	32.10	0.0000

Table S7. Model coefficients of the best model for sesMPD on communities built by environmental filtering, drift and limited dispersal.

	Estimate	Std. Error	t value	Pr($>$|t|)
(Intercept)	0.1367	0.0696	1.96	0.0495
richness	0.0019	0.0011	1.74	0.0811
altitude	-0.2946	0.3949	-0.75	0.4557
I(altitude^2)	-0.0767	0.4124	-0.19	0.8525
richness:altitude	-0.0147	0.0060	-2.47	0.0136
richness:I(altitude^2)	0.0150	0.0061	2.46	0.0141

Table S8. Model coefficients of the best model for sesMPD on communities built by drift and limited dispersal.

	Estimate	Std. Error	t value	Pr($>$|t|)
(Intercept)	0.0018	0.0040	0.44	0.6583

4 — Considerações finais

4.1 Relacionando padrões e processos

4.1.1 Explicação mecanística do padrão

No capítulo 2 desta tese propus uma abordagem pra separar o efeito de processos neutros e de nicho na abundância de espécies de samambaias. A abordagem permite representar processos neutros e de nicho em modelos hierárquicos e, usando de seleção de modelos, inferir quais mecanismos melhor explicam os padrões de abundância de samambaias em comunidades locais. A abordagem permite uma inferência forte – *sensu* McGill (2003) – dado que a partir dela é possível (i) prever muito bem a abundância média das espécies num dado local, e (ii) atribuir a variação das abundâncias a mecanismos neutros e de nicho. Dessa forma, o modelo que melhor explica as abundâncias não apenas tem um bom ajuste aos dados mas também permite uma interpretação mecanística de como as abundâncias locais são definidas a partir do pool de espécies. Um aspecto importante da abordagem é que é possível compreender como as abundâncias médias e a variação em torno das abundâncias são geradas pelos diferentes processos. Assim, para o meu sistema de estudo é possível delimitar como nicho e neutralidade afetam as abundâncias. Retomarei a seguir a explicação do padrão de abundância das espécies construída a partir do modelo.

A explicação que construí a partir do modelo (Figura 4.1) é que existe uma combinação hierárquica de filtros, deriva ecológica e limitação de dispersão afetando a estrutura das comunidades. Primeiro existe um filtro selecionando combinações de atributos – o que aqui chamo de estratégia ecológica – dependendo do local no gradiente altitudinal (Figura 4.1a). Entretanto, ainda passa pelo filtro um conjunto heterogêneo de espécies com maior ou menor fitness. O componente de filtro prevê a média de abundância das espécies que compartilham uma dada estratégia ecológica. A variação de abundância em torno da estratégia ecológica é devido a processos neutros e outros filtros. Por um lado, deriva ecológica e limitação de dispersão em cada montanha fazem as abundâncias das espécies variarem estocasticamente (Figura 4.1b).

Ainda, existe variação das abundâncias das espécies dependendo da posição no gradiente (Figura 4.1c). Esta variação local atribuo a um outro filtro, que chamo de filtro de habitat. Aqui é preciso levantar um ponto importante: este componente de filtro de habitat representa a variação estocástica das abundâncias em cada localidade. A interpretação que proponho é que o filtro de habitat é o componente de filtro não explicado pelas estratégias ecológicas das espécies. Entretanto, é possível que parte da variação na abundância das espécies entre locais seja devido à limitação de dispersão numa escala local. Como o termo que representa este componente é um termo que expressa a variação estocástica de abundância em relação a altitudes, apenas neste caso não é evidente o quanto esta variação é decorrente de filtro independente das estratégias ecológicas explicitadas no modelo ou simplesmente variação estocástica. O que é notável no capítulo 2 é que a inclusão do termo de filtro de habitat aparece em todos os modelos que têm maior peso de evidência. Desse modo, a variação de abundância atribuída ao filtro de habitat é importante para explicar o padrão observado. De maneira geral, a seleção de modelos no capítulo 2 mostra que os componentes que expressam a variação na abundância dos espécies, tanto por processos neutros como de nicho são importantes para explicar os padrões empíricos. No contexto de separar os efeitos de nicho e neutralidade na estruturação de comunidades, parece que compreender quais os mecanismos geram a variação no padrão é crucial.
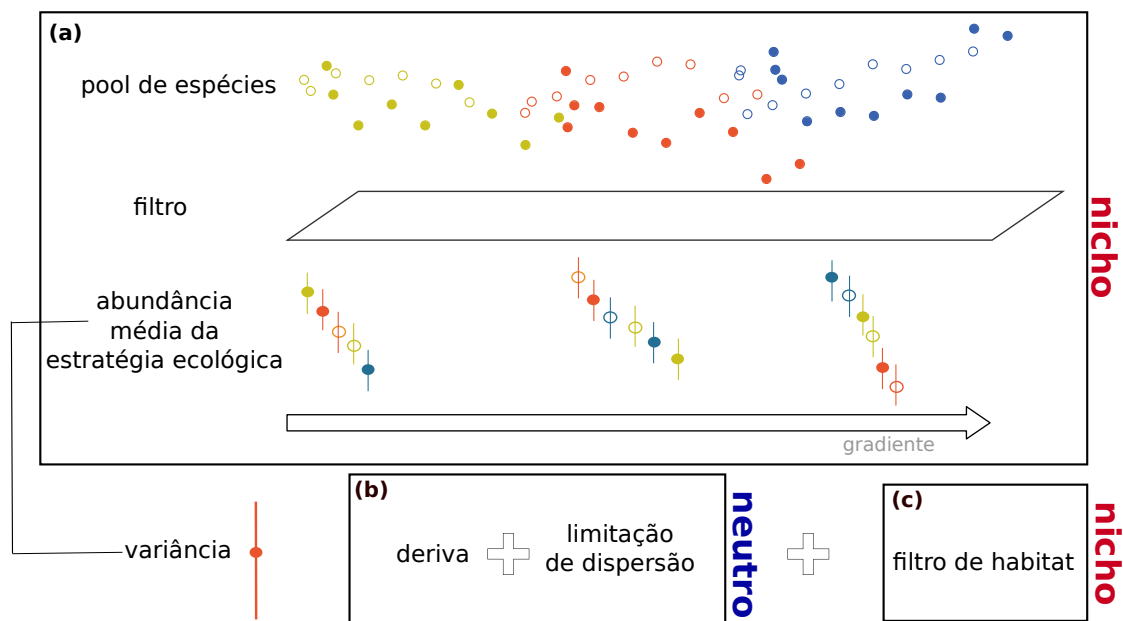

Figura 4.1: Interpretação de como os processos neutros e de nicho geram a partir de um pool de espécies os padrões de abundância observados. (a) Filtro ambiental seleciona as melhores estratégias ecológicas de acordo com o ambiente. A variação de abundância entre espécies que compartilham a mesma estratégia ecológica é devido à (b) deriva e limitação de dispersão e (c) seleção de habitat independente das estratégias ecológicas.

4.1.2 Dos processos ao padrão

A abordagem que propus nesta tese permite construir modelos que representam diferentes processos. A partir destes modelos foi possível gerar cenários em que nicho, neutralidade e a combinação entre nicho e neutralidade afetam comunidades. No capítulo 3 investiguei se os padrões de estrutura filogenética são capazes de refletir os processos pelos quais as comunidades foram geradas, como seria previsto pela abordagem filogenética (WEBB et al. 2002; CAVENDER-BARES et al. 2009). O estudo de caso deste capítulo mostra que (i) filtros ambientais sozinhos geram predominantemente padrões aleatórios de estrutura filogenética e (ii) os processos neutros têm uma assinatura forte no padrão de estrutura filogenética, de modo que comunidades estruturadas por processos neutros e de nicho ou apenas por nicho apresentam um padrão semelhante. O estudo de caso nos mostra que processos de filtro ambiental podem ocorrer independentes da filogenia e que a influência de deriva e limitação de dispersão é capaz de ofuscar um padrão filogenético. Mesmo quando filtro ambiental afeta total ou parcialmente as comunidades, a variação das abundâncias das espécies não pode ser explicada pelos atributos das espécies. Assim, o estudo de caso nos indica que usar apenas um padrão para inferir os processos afetando comunidades não é uma tarefa simples – de fato é um dos objetivos da ecologia de comunidades – e é ainda mais desafiador no contexto em que processos neutros e de nicho operam juntos afetando a estrutura de comunidades.

4.2 Conclusões

O que os capítulos 2 e 3 desta tese nos mostram é que a variação das abundâncias das espécies está sendo explicada em maior parte por deriva e limitação de dispersão. Isto nos leva à questão do quão geral é este padrão, ou como a importância relativa de dispersão ou filtro ambiental variam em diferentes comunidades. A abordagem que propus permitiu aqui identificar para um caso específico simples atributos das espécies que respondem a variações ambientais ao longo dos gradientes altitudinais e o papel da limitação de dispersão na estruturação das comunidades. A abordagem permite também avaliar, em diferentes sistemas, qual a fração das abundâncias das espécies explicada por processos neutros ou de nicho e, assim, compreender como a importância de filtros vs. limitação de dispersão pode variar em comunidades biológicas. Com a ideia atual de que tanto processos neutros e de nicho afetam a estrutura de comunidades (VELLEND et al. 2014), a representação de processos afetando comunidades em efeitos fixos e randômicos em modelos mistos é uma maneira quantitativa de separar os efeitos destes processos. Isto é semelhante à abordagem de partição de variância (GILBERT & LECHOWICZ 2004) que visa separar efeitos de distância e do ambiente na estruturação de comunidades. A roupa nova da abordagem apresentada nesta tese é a possibilidade de sistematicamente confrontar diferentes hipóteses de como as comunidades são estruturadas pelos diferentes processos e traduzir cada um dos processos em componentes de modelos mistos. Com esta abordagem, é possível caminhar no labirinto da ecologia de comuidades (WEIHER & KEDDY 1999) e estabelecer relações entre padrões observacionais de estrutura de comunidades e os processos que os geram.

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Nota sobre as figuras dos capítulos

As figuras utilizadas no cabeçalho dos capítulos são recortes de obras de Piet Mondrian (1872–1944). A obra de Mondrian é de domínio público desde 2015. Mondrian é um dos fundadores do movimento *De Stijl* e conhecido pelo uso de cores primárias e linhas horizontais e verticais. Sempre gostei de sua simplicidade. A obra de Mondrian ilustra esta tese porque ele – como se fosse um ecólogo criando modelos – buscava representar de forma simples elementos da complexidade do mundo.

- **Capítulo 1**
  Composition No. 10 Pier and Ocean, 1915.

- **Capítulo 2**
  Composition C, 1935.

- **Capítulo 3**
  Tree II, 1912.

- **Capítulo 4**
  Composition, 1916.